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Title Page

Regulation mechanism of lanthanum chloride on germination characteristics of wheat (*Triticum aestivum* L.) seeds and physiological response of seedlings

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Abstract: The purpose of this study to investigate the regulatory effects of exogenous lanthanum chloride (LaCl₃) on wheat seed germination and seedling physiological characteristics, in order to screen for the optimal treatment concentration that is most conducive to its growth and development. Wheat seeds were used as experimental materials, and a blank control group (CK) and six gradient treatment groups (T1 to T6) were set up, with three biological replicates in each group. Inoculate 25 seeds into each culture dish and apply 10 mL of LaCl₃ solution at concentrations of 0 (CK), 60, 120, 180, 240, 300, and 360 mg·L⁻¹, respectively, while keeping the filter paper moist. After 3 days of germination, relevant indicators will be measured. In the pot experiment, when the seedling height reaches 5 cm, 10 mL of corresponding treatment solution is sprayed every 3 days. After 20 days of cultivation, the root length, number of fibrous roots, fresh weight, plant height, chlorophyll content, as well as key enzyme activities such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) are measured. The experiment showed that lanthanum chloride exhibited a dual effect of "Minimal stimulation and strong suppression" on wheat growth. Among them, the T4 to T6 groups suffered severe growth inhibition due to excessive concentration, and effective enzyme activity data could not be obtained. Physiological indicators testing showed that compared with the CK group, the low concentration T1 group (60 mg·L⁻¹) significantly increased the activities of SOD,

POD, and CAT by 31.43%, 71.82%, and 69.74%, respectively ($P < 0.05$). The synergistic effect of the medium concentration T3 group ($180 \text{ mg} \cdot \text{L}^{-1}$) was more significant, with the activities of the three enzymes increasing by 44%, 135.16%, and 114.47%, respectively. The chlorophyll content in T1, T2, and T3 groups also significantly increased by 39.84%, 20.86%, and 33.69%, respectively. Correlation analysis revealed that the activities of SOD, POD, and CAT were negatively correlated with seed germination rate, number of fibrous roots, and root length. There was also a significant negative correlation between chlorophyll content and number of fibrous roots. In summary, the optimal concentration for this experiment was $180 \text{ mg} \cdot \text{L}^{-1}$ LaCl_3 treatment. Under these conditions, the germination rate of wheat seeds and the comprehensive physiological growth indicators of seedlings showed the best performance.

Keywords: LaCl_3 , Wheat (*Triticum aestivum* L.), Seed treatment, Seed germination, Seed morphology, Seedling growth, physiological response

1 Introduction

Wheat (*Triticum aestivum* L) belongs to the Triticeae family of the Poaceae family and is an annual or perennial herbaceous plant. Its stem is upright, and the plant height usually has 6-9 nodes. The spike shaped inflorescence stands upright, with flat spikelet shapes on both sides, containing 2 to 5 small flowers. The grains of wheat are mostly oblong in shape, with deep longitudinal grooves on the abdomen. After maturity, they often separate or adhere to the lemma (Feldman et al., 2023; Milla et al., 2024). This crop originated in the "Fertile Crescent" of West Asia, and its domestication history can be traced back to about 10000 years ago (Heun M, et al., 2023). At present, wheat has risen to become the most widely planted and high-yielding food crop in the world, with cultivation areas spanning a wide range from temperate to subtropical regions. In China, as one of the world's major wheat producing countries, the production status of wheat is crucial (Bonjean et al., 2004).

Rare earth elements (REEs) mainly cover 15 lanthanide elements (atomic numbers 57-71) in Group IIIB of the 6th period of the periodic table, and include scandium (Sc) and yttrium (Y) with similar chemical properties, totaling 17 elements. Based on the differences in atomic radius and physicochemical properties, rare earth elements are usually classified into two categories: light and heavy. In recent years, scientific research has confirmed that rare earth elements have significant physiological regulatory effects in the field of agricultural production. At appropriate concentrations, it can not only accelerate crop growth and development, increase yield, and improve quality, but also significantly enhance seed germination potential and germination rate, and positively activate the activity of various key metabolic enzymes. At the same time, rare earth elements can also increase the synthesis of chlorophyll in plants, enhance the efficiency of light energy utilization, thereby strengthening photosynthetic intensity and demonstrating a beneficial regulatory effect on crop growth (Sun et al., 2015).

From the perspective of physiological regulation mechanisms, rare earth elements, as exogenous active regulatory factors, are deeply involved in multiple levels of plant life activities. It can effectively alleviate physiological damage caused by abiotic stress such as salt damage and drought, and maintain the dynamic balance of intracellular reactive oxygen species (ROS) by regulating the antioxidant system, reducing the risk of oxidative stress. In addition, rare earth elements are closely related to the synergy of carbon and nitrogen metabolism, the synthesis of osmoregulatory substances, and energy metabolism processes. At the microscopic level of cells, rare earth elements can regulate ion channel permeability by binding to cell membrane surfaces or membrane proteins, thereby stabilizing membrane structure (Zhang et al., 2013) and ensuring normal material flow and signal transduction in cells. It also contributes to chlorophyll biosynthesis, enhances the accumulation of photosynthetic pigments, and modulates the levels and associated enzyme activities of osmotic regulators like proline and soluble sugars. Through comprehensive intervention in ion transport, osmotic regulation, antioxidant defense, and photosynthetic processes, rare earth elements achieve systematic regulation of plant growth and development.

Lanthanum chloride (LaCl_3), as a typical rare earth compound, has been shown to significantly enhance the activity of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) within a specific concentration range, strengthen the antioxidant defense network of plants, accelerate free radical clearance, and thus improve plant tolerance and adaptability under various stress conditions. Related studies have shown that under optimized treatment concentrations, LaCl_3 can effectively activate the activity levels of key antioxidant enzymes such as SOD, POD, and CAT in plants, improve the function of the antioxidant system, promote efficient clearance of ROS, reduce the damage of oxidative stress to cell structure and metabolic pathways, and thereby enhance the comprehensive resistance and environmental adaptability of plants to stress such as salt and drought.

With the continuous deepening of the application of rare earth resources in agricultural production, their research and application objects have expanded from single crops to diversified crop categories (Wang et al., 2022). Extensive studies have explored rare earth applications in staple grain crops—including Sorghum, millet, barley, oats, rye, buckwheat, barley, potatoes and rice—while large-scale trials have also been carried out in fruit tree cultivation, covering economically important species such as papaya, avocado, wax apple, pomegranate, blueberry, citrus, pineapple, watermelon, and banana. In terms of vegetable cultivation, crops such as tomatoes, eggplants, cucumbers, spinach, lettuce, and peppers have also shown good physiological responses (Zhao et al., 2019). Overall, rare earth elements have shown positive regulatory effects in promoting crop growth, improving quality, and enhancing stress resistance (Wu et al., 2017).

As a type of exogenous active substance with potential, lanthanum chloride has shown great application prospects in regulating plant physiological metabolism, promoting plant growth, and optimizing physiological functions. However, compared to its systematic research on some grains and cash crops, the regulatory mechanism of rare earth lanthanum on the growth and development of wheat seedlings still lacks in-depth exploration. Currently, most research focuses on the description of morphological indicators or growth performance, and there is a relative lack of comprehensive analysis on the dynamic changes of seed germination process (such as germination potential and germination index), as well as the photosynthetic characteristics and physiological and biochemical indicators of seedlings (Zhang et al., 2021). The limitations of this research to a certain extent limit the scientific application and promotion of rare earth elements in green and efficient cultivation systems for wheat.

Numerous studies have demonstrated that applying exogenous regulators—including betaine, salicylic acid, and silicon—can boost the antioxidant enzyme system activity in wheat (Liu et al., 2020), increase ROS clearance efficiency, maintain cellular ion balance (Zheng et al., 2005), and alleviate the damage of stress to photosynthetic structures, thereby improving wheat's stress resistance to a certain extent. While current research predominantly investigates the physiological impacts of conventional mineral nutrients and organic signaling molecules, the role of rare earth elements in modulating wheat growth remains critically underexplored. Although individual reports suggest that low-dose lanthanide elements may have a promoting effect on wheat seed germination, there is a lack of continuous dynamic monitoring covering different developmental stages from germination to seedlings, especially in key areas such as antioxidant enzyme synergistic response mechanisms, photosystem protection pathways, and dose-response relationship thresholds. A systematic and in-depth theoretical explanation has not yet been formed.

Based on the above research background, this study used wheat as the test material and set up lanthanum chloride solutions with different concentration gradients to conduct treatment experiments on seeds and seedlings. During the germination stage, key indicators such as germination rate, relative germination rate, germination potential, relative germination potential, and seed vitality index were measured (Ma et al., 2014) to comprehensively evaluate the effects of lanthanum treatment on seed germination ability and dynamic processes. During the growth period of seedlings, growth indicators such as plant height, fresh weight of aboveground and root systems, biomass accumulation, and root morphology were measured. At the same time, changes in chlorophyll content and the activity of key antioxidant enzymes such as SOD, POD, and CAT were analyzed. By comprehensively analyzing various growth and physiological parameters, the promotion or inhibition effects of different concentrations of lanthanum chloride on wheat germination and seedling development, as well as their evolutionary patterns, are revealed, and the appropriate concentration range is clarified. This study aims to provide theoretical basis and practical reference

for optimizing wheat cultivation and management techniques, enhancing crop stress resistance, and promoting the scientific application of rare earth elements in modern precision agriculture.

2 Material and methods

2.1 Materials

The wheat seeds were supplied by the School of Life Sciences at Huaibei Normal University, and the source of lanthanum, a rare earth element, was lanthanum chloride of analytical grade purity.

2.2 Methods

2.2.1 Seed soaking experiment

Selected wheat seeds with abundant grains and uniform size as experimental materials. Firstly, disinfect the surface of the seeds with 75% ethanol for 30 seconds, and then rinse them 5 times with sterile water to remove residual alcohol. The disinfected seeds were immersed in different concentrations of lanthanum chloride (LaCl_3) solution for seed soaking treatment. The experiment set up a completely blank control group (CK) and 7 treatment levels (T1-T6), with 3 biological replicates for each treatment and 20 seeds placed in each dish. The concentrations of lanthanum chloride used in each treatment were 0, 60, 180, 240, 300, and 360 $\text{mg}\cdot\text{L}^{-1}$, respectively. 10 mL of the corresponding treatment solution was added to the culture dish each time to keep the filter paper moist. After 3 days of cultivation, statistics and measurement of seed germination related indicators will begin. Select disposable culture dishes with a diameter of 9 cm for seed soaking experiments, and conduct pot experiments using plastic pots with a diameter of 25 cm $\times$ 12 cm $\times$ 12 cm.

2.2.2 Potting Experiment

Following the sieving of vermiculite, it was subjected to high-pressure sterilization at 120°C for 20 minutes and subsequently allowed to dry naturally. Sand and vermiculite were then mixed in a 1:1 volume ratio and placed into flower pots, with each pot containing 720 grams of the mixture. Whole wheat seeds were selected and soaked in lanthanum chloride (LaCl_3) solutions with concentrations of 0 (CK), 60, 120, 180, 240, 300, and 360 $\text{mg}\cdot\text{L}^{-1}$ for 2 hours. The corresponding treatment groups were designated as CK, T1, T2, T3, T4, T5, and T6. Subsequently, the seeds were uniformly sown in plastic pots with a diameter of 9 centimeters and a depth of approximately 2 centimeters, and these pots were placed in a location with ample sunlight and suitable temperature for cultivation. Every three days, 10 milliliters of purified water was added to each pot. After one week of germination, when the plant height reached approximately 5 cm, each experimental group was established with three biological replicates. These replicates were treated with an equal volume of LaCl_3 solution every three days for a total of five treatments, after which various physiological indicators were measured and analyzed.

2.2.3 Germination Index Assay

Germination phase, the germination dynamics were observed and recorded at regular intervals every day, and the effective germination was determined based on the breakthrough of the embryonic root through the seed coat and a population germination rate of over 80%. Calculate the germination potential and germination rate on the 4th and 7th day of germination, and further calculate the germination damage rate, germination index, and relative germination index. The calculation of various indicators is carried out according to the research method of ISTA (ISTA et al. 2023) and Liu (2026), as follows:

Germination Potential (%) = (Number of seeds germinated within 3 days / Total number of tested seeds) × 100%, reflected the speed and uniformity of seed germination, indicating seed vigor.

Germination Rate (%) = (Number of seeds germinated within 7 days / Total number of tested seeds) × 100%, measured the overall germination capacity over a standard 7-day period.

Germination Damage Rate (%) = $[(N_c - N_t) / N_c] \times 100\%$, where N_c = total number of germinated seeds in the control group, N_t = total number of germinated seeds in the treatment group. Indicated the inhibitory effect of a treatment on germination.

Germination Index = $\sum (G_t / D_t)$, G_t = number of seeds germinated on day t , D_t = corresponding day of germination (e.g., day 1, 2, 3...).

A weighted were measured that emphasized early germination, reflecting both speed and progression.

Relative Germination Index (%) = (Germination Index of treatment group / Germination Index of control group) × 100%, used to compare treatment effects relative to the control, assessing phytotoxicity or stimulatory impacts.

2.2.4 Assessment of growth and physiological parameters

On day 7 of germination, seedling growth parameters: including main root length, plant height, fibrous root number, and fresh weight were recorded. Superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities in leaves were assayed by NBT, guaiacol, and UV absorption methods, respectively.

2.3 Statistical Analysis

Data were expressed as mean values ± standard deviations (SD) from five replicates (plants). Statistical analyses were performed using IBM SPSS 25.0 (IBM Corp., Armonk, NY, USA) and Microsoft Excel 2010 (Redmond, USA), with Excel used for data entry and SPSS employed to examine the relationships between seed germination and the growth and physiological traits of chilling-stressed seedlings. A two-way analysis of variance (ANOVA) with Bonferroni post hoc tests was applied to assess differences, where * indicates $p < 0.05$ and ** indicates $p < 0.01$. All tests for statistical significance were conducted at the $p \leq 0.05$ level.

3 Results

3.1 The effect of soaking wheat seeds in different concentrations of lanthanum chloride solution on seed germination

3.1.1 Seed germination morphology

From Figure 1, it can be seen that different concentrations of LaCl_3 treatment had a significant dose-response effect on wheat seed germination. The overall trend was characterized by low concentration promotion and high concentration inhibition. The germination rate of seeds was highest under T1 treatment, and the uniformity and growth potential of seedlings showed the best performance, which was significantly better than the T2 treatment level. T4 and T5 treatments followed closely, while T6 treatment had the weakest effect and relatively poor germination performance.

Comprehensive analysis showed that lanthanum chloride at T1 concentration had the most significant promoting effect on wheat seed germination. This may be related to the ability of appropriate concentrations of lanthanum element to enhance internal metabolic activity of seeds, activate related hydrolytic and antioxidant enzyme systems, thereby accelerating material conversion and energy supply, and improving germination efficiency. When the concentration is too high, it may have a certain stress effect on cells, thereby inhibiting the germination process.

3.1.2 Seed germination index

The T1 group exhibited the highest germination rate (Figure 2) and germination potential (Figure 3), indicating that $60 \text{ mg} \cdot \text{L}^{-1}$ lanthanum chloride treatment had the most pronounced positive effect on wheat seed germination. Compared to the CK group (96%), the T1 group achieved a 100% germination rate ($P < 0.05$). As LaCl_3 concentration increased, germination rates across treatment groups followed a biphasic trend—initial enhancement followed by inhibition—in the order: $\text{T1} > \text{CK} > \text{T2} (92\%) > \text{T3} (88\%) > \text{T4} (81\%) > \text{T5} (74\%) > \text{T6} (73\%)$. Similarly, germination potential displayed an initial rise and subsequent decline, ranking as $\text{T1} (100\%) = \text{CK} > \text{T2} (96\%) > \text{T3} (87\%) > \text{T4} (80\%) > \text{T5} (72\%) > \text{T6} (66\%)$. Compared with the control group (CK), no significant difference in germination damage rate was observed under low-concentration lanthanum chloride treatments across groups T1, T2, T3, and T4. When the concentration was increased to T6 level ($300\text{-}360 \text{ mg} \cdot \text{L}^{-1}$), the germination damage rate was significantly higher than that of CK, indicating that lanthanum chloride in this concentration range has an inhibitory effect on seed germination and can effectively reduce germination rate. Its mechanism of action may involve multiple physiological levels of interference: ion competition leads to nutrient absorption disorders: La^{3+} , as a trivalent cation, competes with essential plant nutrients such as Ca^{2+} , K^+ , Mg^{2+} for membrane transport protein binding sites, interfering with their transmembrane absorption and intracellular distribution, disrupting ion homeostasis, weakening membrane system stability and related metabolic enzyme activity, ultimately affecting the physiological and metabolic basis of early seed germination. Inducing oxidative stress damage to cellular structure: High concentrations of La^{3+} can activate the intracellular reactive oxygen species (ROS) generation system, leading to excessive accumulation of superoxide anions, hydrogen

peroxide, and other substances. ROS attacks membrane lipids, proteins, and DNA, causing membrane lipid peroxidation, enzyme inactivation, and genetic material damage, disrupting the structural integrity of embryonic cells, and thereby inhibiting the germination process. Inhibition of key enzymes for mobilizing stored substances: La^{3+} can directly or indirectly inhibit the activity of hydrolytic enzymes such as amylase and protease, hinder the degradation of starch and protein in endosperm, reduce the supply of energy and building materials required for germination such as soluble sugars and amino acids, cause metabolic stagnation, and prevent seeds from successfully completing germination initiation. Disrupting the hormone signaling regulatory network: Rare earth elements may interfere with the synthesis, transport, or signal transduction of endogenous hormones such as gibberellin and auxin, weakening the regulatory effects of hormones on processes such as endosperm and embryonic root elongation, leading to delayed or abnormal germination. Disrupting membrane integrity leads to intracellular substance leakage: High concentration LaCl_3 treatment can damage the membrane structure, increase membrane permeability, cause electrolyte and organic molecule leakage, disrupt intracellular homeostasis, further exacerbate physiological dysfunction, and inhibit seed germination.

3.2 The effect of different concentrations of LaCl_3 solution treatment on the growth physiology of wheat seedlings

3.2.1 Changes in height, root length, leaves, and fresh weight of wheat seedlings

This study observed that different concentrations of lanthanum chloride had differential effects on the growth morphology of wheat seedlings (Figure 4A and 4B). Compared with the control group, T1 treatment ($60 \text{ mg}\cdot\text{L}^{-1}$) significantly promoted leaf elongation, reaching its maximum length (Figure 5B). The plants under T2 treatment ($120 \text{ mg}\cdot\text{L}^{-1}$) were the shortest. T3 treatment ($240 \text{ mg}\cdot\text{L}^{-1}$) induced the least number of fibrous roots (Figure 5C). The control group maintained optimal levels in average root length and plant height (Figure 5C and 5A). There was no significant difference in leaf length between the T1 to T3 treatment groups. When the treatment concentration reaches or exceeds $240 \text{ mg}\cdot\text{L}^{-1}$, plant growth is strongly inhibited, manifested as almost stagnant growth of seedlings in the T4 ($300 \text{ mg}\cdot\text{L}^{-1}$), T5 ($360 \text{ mg}\cdot\text{L}^{-1}$), and T6 ($420 \text{ mg}\cdot\text{L}^{-1}$) treatment groups. From the trend of plant height changes, the plant height showed a continuous decreasing trend from the control group to the T3 group, suggesting that higher concentrations of LaCl_3 stress may inhibit seedling growth by overactivating the plant's antioxidant defense system and forcing adaptive adjustments in energy metabolism. The analysis of specific growth indicators showed that under high concentration stress, the root elongation of T3 group was significantly inhibited, and the root length was significantly shortened by 28.08% compared to the control group ($P < 0.05$). The leaf length showed a fluctuation of first decreasing and then increasing between groups T1 and T3, but the overall change amplitude was not significant, and the difference with the control group was not significant. The number of fibrous roots in all treatment groups was lower than that in the control group. It is worth noting that the fresh weight of seedlings reached its peak in group T1 (Figure 5D), which was significantly increased by 20.83%

compared to the control group ($P < 0.05$). This result indicates that the treatment with $60 \text{ mg} \cdot \text{L}^{-1}$ lanthanum chloride is most beneficial for the synthesis and accumulation of organic matter in wheat seedlings.

3.2.2 Changes in antioxidant enzyme activities of wheat seedlings under different concentrations of LaCl_3 treatment

This study further analyzed the effects of different concentrations of lanthanum chloride treatment on the antioxidant enzyme system of wheat seedlings. The results showed that as the treatment concentration increased, the activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) all exhibited a response pattern of first increasing and then decreasing (Figure 6A, 6B, 6C). Specifically, SOD activity peaked under the T3 treatment ($180 \text{ mg} \cdot \text{L}^{-1}$), reaching $50.4 \text{ U} \cdot \text{g}^{-1} \cdot \text{FW} \cdot \text{min}^{-1}$ —a 44.0% increase over the control group ($35 \text{ U} \cdot \text{g}^{-1} \cdot \text{FW} \cdot \text{min}^{-1}$). Similarly, POD and CAT activities reached their highest levels in the T3 group, at $94.3 \text{ U} \cdot \text{g}^{-1} \cdot \text{FW} \cdot \text{min}^{-1}$ and $32.6 \text{ U} \cdot \text{g}^{-1} \cdot \text{FW} \cdot \text{min}^{-1}$, respectively, representing increases of 135.16% and 114.47% compared to the CK group. Across the T1 to T3 range ($60\text{--}180 \text{ mg} \cdot \text{L}^{-1}$), the activities of all three antioxidant enzymes were significantly elevated relative to the control ($P < 0.05$), aligning with the improved seedling morphological traits observed earlier. This indicates that an optimal concentration of LaCl_3 can effectively enhance the plant's antioxidant defense system. Further analysis showed that the SOD activity was at its highest level under T3 treatment, suggesting that this concentration may coordinate the regulation of the SOD-POD-CAT synergistic network to more efficiently eliminate accumulated reactive oxygen species and free radicals in the body, thereby promoting growth while maintaining stress resistance and achieving the optimal balance between growth and stress response.

3.2.3 Changes in Chlorophyll Content of Wheat Seedlings under Different Concentrations of LaCl_3 Treatment

Different concentrations of lanthanum chloride treatment also had a significant effect on the photosynthetic pigment content of wheat seedling leaves. As the concentration of treatment increases, chlorophyll a, chlorophyll b, and total chlorophyll content all show a pattern of first increasing and then decreasing, exhibiting a typical "low promotion, high inhibition" dose-response relationship (Figure 7A, 7B, 7C).

Specifically, the total chlorophyll content reached its maximum value at T1 treatment ($60 \text{ mg} \cdot \text{L}^{-1}$), which was 0.523 mg/g , a significant increase of 39.84% ($P < 0.05$) compared to the control group (0.374 mg/g). This indicates that a suitable concentration of LaCl_3 can effectively promote chlorophyll biosynthesis process. However, when the concentration was increased to T3 treatment ($180 \text{ mg} \cdot \text{L}^{-1}$), the total chlorophyll content decreased to 0.5 mg/g , a decrease of 33.69% compared to the control group, indicating the inhibitory effect of high concentration LaCl_3 on chlorophyll synthesis.

The changes in the content of this photosynthetic pigment directly affect the

photosynthetic capacity of the plant. The inhibition of chlorophyll synthesis leads to a decrease in photosynthetic efficiency, resulting in chlorosis and yellowing of plant leaves, limited growth in plant height, and a significant reduction in biomass accumulation. The above results further confirm the stress effects of high concentrations of rare earth elements on plant growth and development.

3.2.4 Correlation analysis of physiological and growth indicators of wheat seedlings under different concentrations of LaCl₃ treatment

Correlation analysis of the physiological and growth indices in seedlings treated with varying concentrations of LaCl₃ (as shown in Table 1) revealed that SOD enzyme activity exhibited a negative correlation with plant root length ($r = -0.900$), seed germination rate ($r = -0.690$), and the number of fibrous roots ($r = -0.849$). The activity of POD enzyme is highly negatively correlated with seed germination rate ($r = -0.802$) and number of fibrous roots ($r = -0.988^*$), and negatively correlated with seedling root length ($r = -0.976^*$). CAT enzyme activity is negatively correlated with seed germination rate ($r = -0.774$) and number of fibrous roots ($r = -0.940$), and negatively correlated with seedling root length ($r = 0.950$). There is a highly significant negative correlation between chlorophyll content and the quantity of fibrous roots ($r = -0.967^*$), as well as a negative correlation between chlorophyll content and root length ($r = 0.887$).

4 Discussion

Seed germination is the initial stage of crop life cycle and is highly sensitive to changes in environmental factors. Seed germination quality directly dictates subsequent plant growth. Lanthanum, a typical rare earth element, is widely used in agriculture for its small hydrated ion radius, high chemical activity, and low biological toxicity (Yang et al. 2017). It is often used to improve crop yield and stress resistance. La⁺ has a high charge density and strong coordination ability, making it easy to bind to specific sites of intracellular biomolecules and the inner membrane system (Lin et al. 2022), thereby affecting membrane system stability and cell signaling pathways, regulating related gene expression and physiological metabolic processes.

There have been many research reports on the regulatory effects of rare earth elements on seed germination. Liu et al. (2010) confirmed that soaking seeds in lanthanum nitrate can significantly promote the growth of wheat seedlings, manifested by an increase in seedling height, root shoot ratio, and leaf area (Liu et al. 2010). He et al. (2005) used Sandalwood as a material and found that soaking seeds in rare earth solution could improve seed germination rate, but the germination potential showed a decreasing trend with increasing concentration, and there was an optimal working concentration (He et al. 2005), which is consistent with most research conclusions. Zhou et al. (2003) confirmed through a sodium nitrate control experiment that La³⁺ is the core factor promoting seed germination, and speculated that its mechanism of action is related to regulating seed water absorption rate, seed coat permeability, respiratory metabolism, and endogenous hormone levels.

The above studies indicate that lanthanum has a significant dose-response effect on seed germination and seedling growth, with low concentrations promoting and high concentrations inhibiting. Its regulatory mechanism involves multiple levels such as cell signal transduction, membrane structure integrity, and metabolic processes. Using wheat as the experimental material, this study systematically explored the impacts of varying concentrations of lanthanum chloride on seed germination, seedling growth, and physiological parameters. The results showed that LaCl_3 exhibited an overall inhibitory effect on wheat seed germination and seedling growth, and the degree of inhibition increased with increasing concentration. The germination rate and germination potential showed a gradient decreasing trend.

From the analysis of its mechanism of action, La^{3+} can interfere with seed germination and seedling establishment through multiple pathways. Firstly, La^{3+} easily binds to proteins and nucleic acids in seeds, altering cell membrane permeability and affecting water absorption efficiency (Zhou et al. 2003), hindering the normal initiation of embryonic roots and embryos. Secondly, La^{3+} can inhibit the activity of key germination enzymes such as α -amylase and protease, leading to hindered starch and protein degradation in the endosperm, insufficient energy and material supply, and thus delaying the germination process.

At the cellular structure level, high concentrations of La^{3+} will compete with ions to replace essential ions such as Ca^{2+} and Mg^{2+} that maintain membrane stability, disrupting the integrity of the embryonic cell membrane, causing extracellular material leakage, inhibiting cell division in the root meristematic zone and elongation of the embryo sheath, ultimately leading to a decrease in germination rate and vigor. As the core organ for nutrient absorption, the function of the root system is also significantly affected: La^{3+} inhibits the activity of root tip meristematic zone and H^+ -ATPase, interferes with the active absorption of nutrients such as N, P, K, etc., leading to a shortage of aboveground material supply, manifested as a decrease in plant height, root length, and biomass.

Damage to the photosynthetic system is another important reason for the inhibition of seedling growth. La^{3+} can inhibit the activity of key enzymes involved in chlorophyll synthesis, such as δ -aminolevulinic acid synthase, disrupt the ultrastructure of chloroplasts, leading to a decrease in chlorophyll content and photosynthetic efficiency. The reduction in photosynthetic products further limits the growth of seedlings. In addition, La^{3+} can also interfere with endogenous hormone balance: inhibit polar transport of auxin, hinder root tip elongation. Reducing the content of gibberellin weakens the positive regulatory signal of germination and exacerbates germination delay (Xu et al. 2017).

This study investigated the effects of varying LaCl_3 concentrations on wheat seed germination, seedling growth, and physiological traits. Results revealed that 60

mg·L⁻¹ was the optimal concentration, yielding the highest germination rate and vigor. This was attributed to LaCl₃'s role in regulating seed enzyme activity and endogenous hormone levels, activating antioxidant systems to facilitate germination. However, when concentrations exceeded 120 mg·L⁻¹, germination rates declined progressively, with a notable inhibitory effect observed at 360 mg·L⁻¹, indicating a dual effect where low concentrations promote germination while medium to high concentrations suppress it. High LaCl₃ levels may hinder water absorption during germination, thus impeding seed sprouting (Zhou et al. 2019). Findings align with prior studies: appropriate rare earth concentrations enhanced cotton seed germination indices (Fang et al. 2002) and boosted rice seed water absorption, respiration, and metabolism. This research corroborates such results, offering valuable insights for the rational application of rare earth elements in agricultural practices.

Simultaneously, this study indicates that different concentrations of lanthanum chloride have varying degrees of effects on the root system, leaf length, leaf width, plant height, and fresh weight of wheat. Specifically, CK has the longest average root length, the highest average number of fibrous roots and plant height, and the longest average T1 fresh weight and leaf length. However, there is no significant difference in each indicator group.

Under the treatment of 60 mg·L⁻¹ LaCl₃, the root development of seedlings showed almost no change, but slightly decreased. At the same time, the synthesis ability of chlorophyll a was significantly improved compared to the control group CK. Under the treatment conditions of 120-180 concentration LaCl₃, the root development of seedlings was inhibited to a certain extent. The chlorophyll a content in T2 treatment reached a peak of 0.386, with an increase of 86.47%. Mechanistically, this promotion may arise from La³⁺ mimicking calcium signaling to activate photosynthesis-related genes (e.g., Lhcb family) and boost magnesium transmembrane transport, facilitating chlorophyll precursor synthesis. Low-dose La³⁺ may also regulate endogenous hormones, such as raising cytokinin/abscisic acid ratio, delaying chloroplast aging to sustain high photosynthetic efficiency.

However, high-concentration LaCl₃ significantly inhibited seedling growth, with T4-T6 groups showing almost no growth and losing photosynthetic capacity. Three mechanisms may underlie this: La³⁺ competitively occupies chlorophyll synthase's active center, impairing its catalytic function. it disrupts thylakoid membrane lipid bilayer order, damaging the photosynthetic membrane system. it induces massive reactive oxygen species (ROS) accumulation, accelerating D1 protein degradation. Meanwhile, malondialdehyde (MDA) accumulation forms a vicious cycle: chloroplast damage increases electron leakage, triggering superoxide anion outburst, exacerbating lipid peroxidation, and ultimately causing thylakoid membrane collapse.

Wheat seedlings also exhibited distinct physiological variations under different LaCl₃ concentrations. Antioxidant enzyme activities differed across groups: compared with

the control, SOD, POD, and CAT activities in the T1-T3 groups rose with increasing LaCl₃ concentration. SOD activity peaked at 50.4 U·g⁻¹·FW·min⁻¹ in the T3 group, demonstrating a clear positive concentration-dependent response. CAT activity showed a weak concentration response, increasing from 25.8 U·g⁻¹·FW·min⁻¹ in T1 group to 32.6 U·g⁻¹·FW·min⁻¹ in T3 group, an increase of 26.36%. This reflects the specific induction effect of low concentration LaCl₃ on CAT activity, especially in the range of 60-180 mg·L⁻¹, where the three enzymes synergistically increased, indicating that the antioxidant enzyme defense network is effectively activated and jointly enhances the ability to clear reactive oxygen species. Against adversity, SOD acts as the first antioxidant line, scavenging superoxide radicals into H₂O₂. CAT, most effective for H₂O₂ removal, peaks early. POD works later. Sustained high SOD/CAT activity triggers membrane lipid peroxidation. Their dynamic changes reveal distinct antioxidant mechanisms under varying LaCl₃ concentrations (Liu et al, 2018).

Low-dose LaCl₃ significantly boosts SOD activity (Li et al. 2020), scavenging O₂⁻ to mitigate membrane damage and promote root growth, likely by stabilizing SOD via zinc finger domain binding. Under high concentration LaCl₃ stress, the activity of peroxidase (POD) continues to increase, maintaining the stability of the membrane system by efficiently decomposing H₂O₂. SOD and POD together form a closely coordinated "SOD-POD cascade defense network": SOD is responsible for converting O₂⁻ to H₂O₂, while POD further reduces it to H₂O, thus completing the cascade clearance of reactive oxygen species. This result also validates the "antioxidant enzyme function conversion" theory proposed by relevant scholars (Zhang et al. 2023), which indicates that SOD takes on a leading defensive role when plants are exposed to mild stress, whereas POD becomes the core player in reactive oxygen species (ROS) scavenging under severe stress conditions (Liu et al. 2018). Nevertheless, this shift in enzyme activity comes with associated metabolic trade-offs. Specifically, high concentrations of LaCl₃ trigger a dramatic surge in POD activity. This heightened activity demands a substantial supply of reducing power in the form of NADPH. The increased consumption of NADPH may then impede the process of photosynthetic carbon assimilation, as it creates competition for the carbon sources required for both the POD-mediated ROS scavenging and the carbon fixation reactions in photosynthesis.

Furthermore, the antioxidant enzyme system of seedlings exhibits a typical concentration-dependent response under LaCl₃ stress. When treated with low concentrations (60-120 mg·L⁻¹) of lanthanum chloride, the activity of superoxide dismutase (SOD) is specifically induced and enhanced. This elevated SOD activity effectively scavenges superoxide anions (O₂⁻), mitigates membrane lipid peroxidation damage, and establishes a favorable redox environment that promotes root growth. (Chen et al. 2018). When the concentration was increased to 120-180 mg·L⁻¹, the activity of peroxidase (POD) was significantly enhanced, and its functional core shifted to the decomposition of hydrogen peroxide (H₂O₂) catalyzed by SOD to maintain the stability of cell membrane structure. The sequential activation and

functional relay of SOD and POD together form a sophisticated 'cascade defense network' to adapt to oxidative stress of different intensities.

Plant growth and physiological indicators mirror its growth, development and environmental adaptability, and correlation analysis helps explore their internal relationship. In this experiment, the activities of SOD, POD, and CAT enzymes were negatively correlated with root length and the number of fibrous roots in terms of antioxidant enzymes and growth indicators. This phenomenon may be related to the increased activity of SOD, POD, and CAT enzymes in the early stage of seed growth, which inhibits relevant growth hormones to affect seed germination and root elongation. Under La^{3+} stress, chlorophyll content shows a significant negative correlation with fibrous root number and length. The core reason is that La^{3+} "targeted inhibition" on roots and compensatory maintenance of leaf chlorophyll synthesis coexist. La^{3+} can directly weaken the root system's elongation ability (root length shortening) and absorption ability (ion adsorption, water transport obstruction) through ion competition (replacement of essential ions such as Ca^{2+} and K^{+} on the root cell membrane) and damage to cell structure (such as damaging root hair cells and inhibiting cell division in the root tip meristematic zone). At this point, although plants are still synthesizing chlorophyll, the growth and function of their roots have been significantly inhibited. To alleviate the potential damage of La^{3+} to the leaf photosynthetic system, plants may prioritize maintaining chlorophyll synthesis (such as by increasing chlorophyll synthase activity and precursor material supply) to preserve photosynthetic efficiency. But this "compensation" did not translate into resource investment in the root system-instead, due to the direct toxicity of La^{3+} to the root system, root growth lagged, ultimately resulting in the phenomenon of "high chlorophyll content, weak root length and absorption capacity". This situation is essentially a "stress imbalance" in plants under La^{3+} stress: chlorophyll synthesis in leaves is enhanced due to "self-protection" (Huang et al. 2016), but root growth and function are inhibited due to "toxic damage", resulting in a mismatch between their growth rhythm and resource allocation.

This study found that when the concentration of LaCl_3 exceeded $120 \text{ mg}\cdot\text{L}^{-1}$, the germination rate of wheat gradually decreased, and the inhibitory effect was particularly significant at $360 \text{ mg}\cdot\text{L}^{-1}$. This is consistent with the research results of Wang et al. (2011) under simulated acid rain conditions, which quantified the dose-response of LaCl_3 on wheat germination rate, root activity, and chlorophyll content, further confirming the inhibitory effect and related physiological mechanisms of high concentration lanthanum. In this study, different concentrations of LaCl_3 had varying effects on wheat root system, plant height, fresh weight, and other indicators. The control group (CK) had the best root length and number of fibrous roots, the T3 group had the highest plant height, and the T1 group had the highest fresh weight and leaf length. However, there was no significant difference between the treatments.

Under the treatment of $60\text{-}120 \text{ mg}\cdot\text{L}^{-1}$ low concentration LaCl_3 , the elongation of

wheat seedling hypocotyls and root development were slightly inhibited, but the chlorophyll synthesis ability was improved. Among them, the T2 group (120 mg·L⁻¹) had a chlorophyll a content of 0.386 mg/g, which was significantly increased by 86.47% compared to the control group. This effect may be related to the simulated calcium ion signaling pathway by La³⁺: as a Ca²⁺ analogue, La³⁺ can activate the expression of photosynthetic genes such as the Lhcb gene family, enhance magnesium ion transmembrane transport, and promote chlorophyll precursor synthesis. Simultaneously regulating the proportion of endogenous hormones, delaying chloroplast aging, and maintaining photosynthetic function. As the concentration further increases, the inhibitory effect of LaCl₃ on seedling growth becomes prominent, and plant growth stagnates, exhibiting a typical "low promotion, high inhibition" characteristic.

From physiological perspective, the antioxidant enzyme activity of wheat seedlings shows a regular response to changes in LaCl₃ concentration. Compared with the control group, the activities of SOD, POD, and CAT in the T1-T3 group increased with increasing concentration, with SOD reaching a peak of 50.4 U·g⁻¹·FW·min⁻¹ in the T3 group (180 mg·L⁻¹), and CAT activity increasing from 25.8 U·g⁻¹·FW·min⁻¹ in the T1 group to 32.6 U·g⁻¹·FW·min⁻¹ in the T3 group, an increase of 26.36%, indicating that low concentration LaCl₃ can specifically induce CAT activity. Within the concentration range of 60-180 mg·L⁻¹, the three enzymes synergistically upregulated, activating the antioxidant defense network and enhancing the ability to clear reactive oxygen species.

When plants respond to stress, the antioxidant enzyme system plays a synergistic role: SOD acts as the first line of defense, dismutating superoxide anions (O₂⁻) into hydrogen peroxide (H₂O₂). CAT efficiently decomposes H₂O₂ in the early stages of stress, while POD is cleared in the later stages. The dynamic changes of SOD, CAT, and POD reflect the differential response mechanism of wheat antioxidant system to different concentrations of LaCl₃ stress.

At the regulatory level, a suitable concentration of LaCl₃ can enhance SOD activity, clear O₂⁻, alleviate membrane lipid peroxidation, and promote root elongation. The mechanism may be the binding of La³⁺ to the zinc finger structure of the SOD active center, improving enzyme protein stability and catalytic efficiency. At the same time, SOD and POD form a synergistic clearance system, constructing a cascade pathway for reactive oxygen species clearance, and verifying the hypothesis of "antioxidant enzyme function conversion".

Correlation analysis shows that the activities of SOD, POD, and CAT are negatively correlated with root length, number of fibrous roots, and seed germination rate. This may be due to the upregulation of antioxidant enzyme activity during early germination, which inhibits the action of growth hormone and interferes with the process of germination and root elongation, reflecting the intrinsic relationship

between growth phenotype and physiological response.

5 Conclusions

In summary, this study indicates that exogenous lanthanum chloride has an overall inhibitory effect on wheat seed germination and seedling growth. Among them, the control group (CK) treatment showed the best germination and growth indicators, as well as the best performance in root system, plant height, fresh weight and other traits. Low concentrations of LaCl_3 (T1-T3 groups) can increase the chlorophyll content of wheat, and the activities of SOD, POD, and CAT show an upward trend with increasing concentration. The three enzymes form a highly efficient and synergistic dynamic balance, enabling wheat seedlings to achieve a better physiological balance between growth promotion and stress resistance.

Declarations

Ethics Approval: Not applicable.

Authors' Contribution Statements: Chun Liu was responsible for experimental design and manuscript writing, Wu Chen, Caiyan Dong and Zihao Ding implemented the experimental content, and corrected and revised the paper.

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Consent to Participate: On behalf of all the authors, the corresponding author declares consent to participate in this article.

Consent for Publication: On behalf of all the authors, the corresponding author declares consent to the publication of this article in the Seed Science and Technology.

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Figure 1 The germination status of wheat (*Triticum aestivum* L) seeds under different treatments

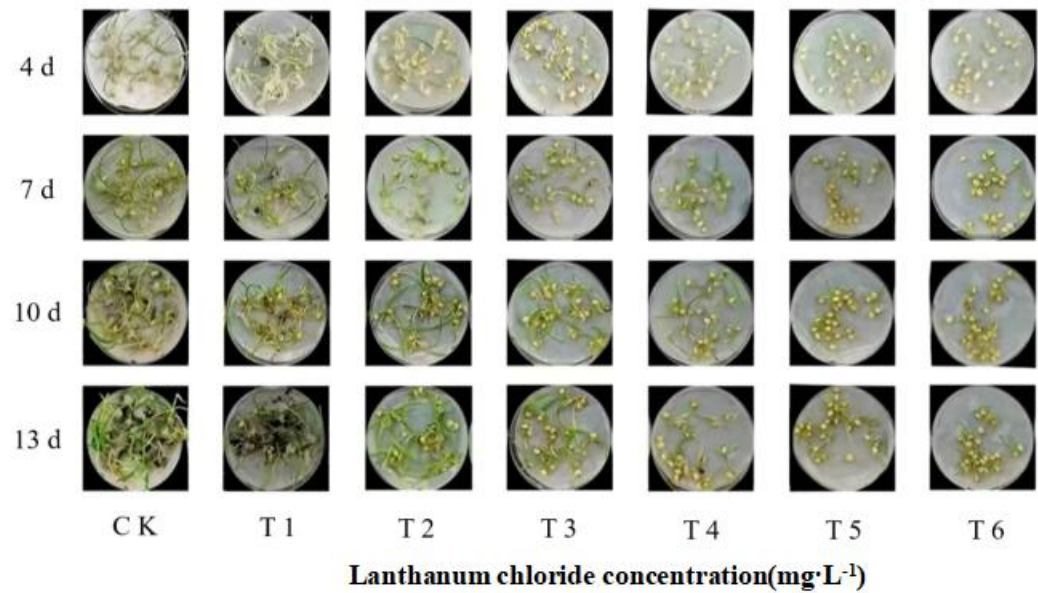


Figure 2 Germination rate of wheat seeds

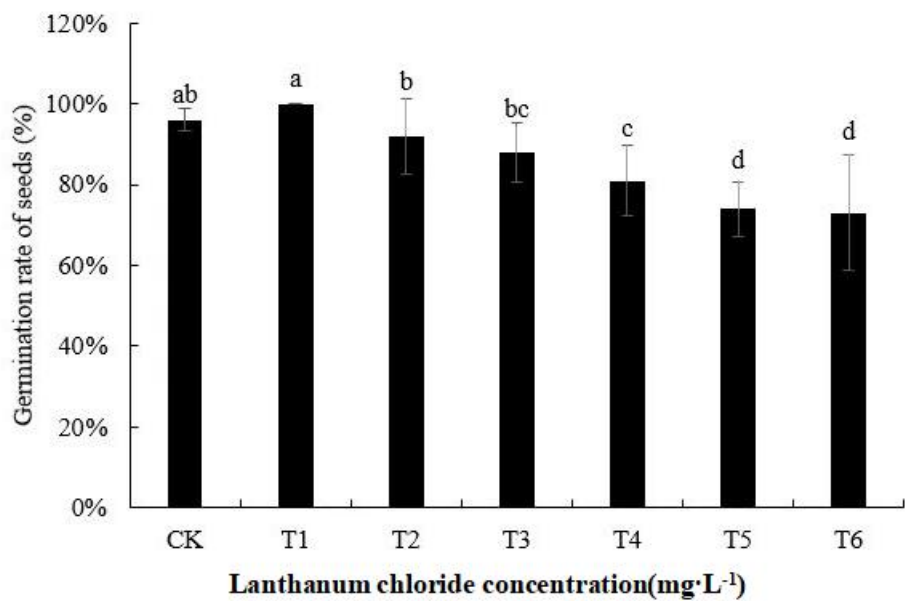


Figure 3 Germination potential of wheat seeds

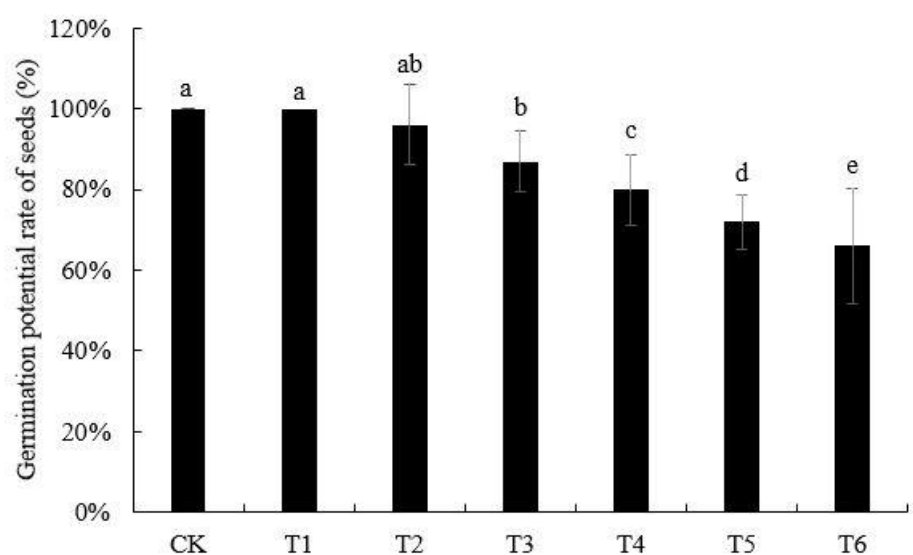


Figure 4 Seedling phenotypes under different LaCl_3 concentrations, (A) Top view of wheat growth, (B) Longitudinal diagram of wheat growth

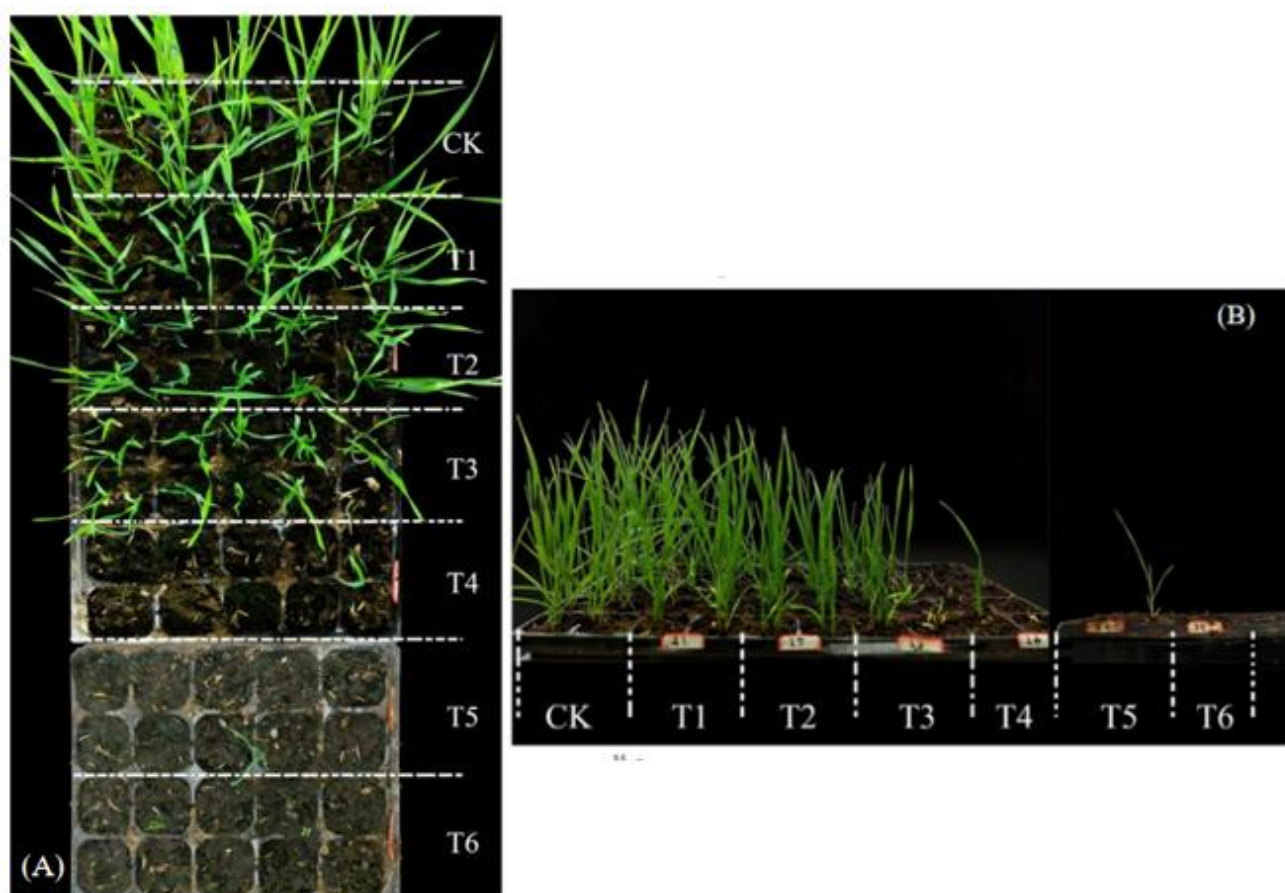


Figure 5 Changes of seedling morphology and fresh weight

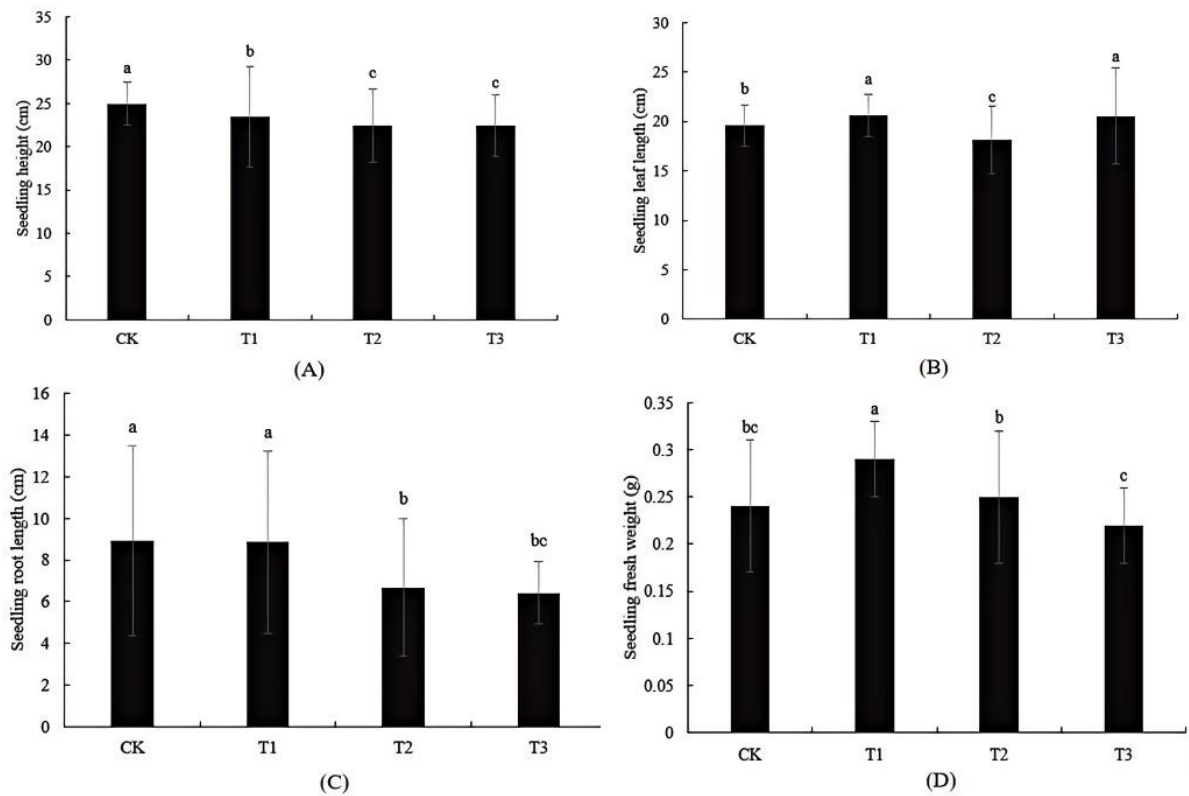


Figure 6 antioxidant enzyme activities in wheat seedling

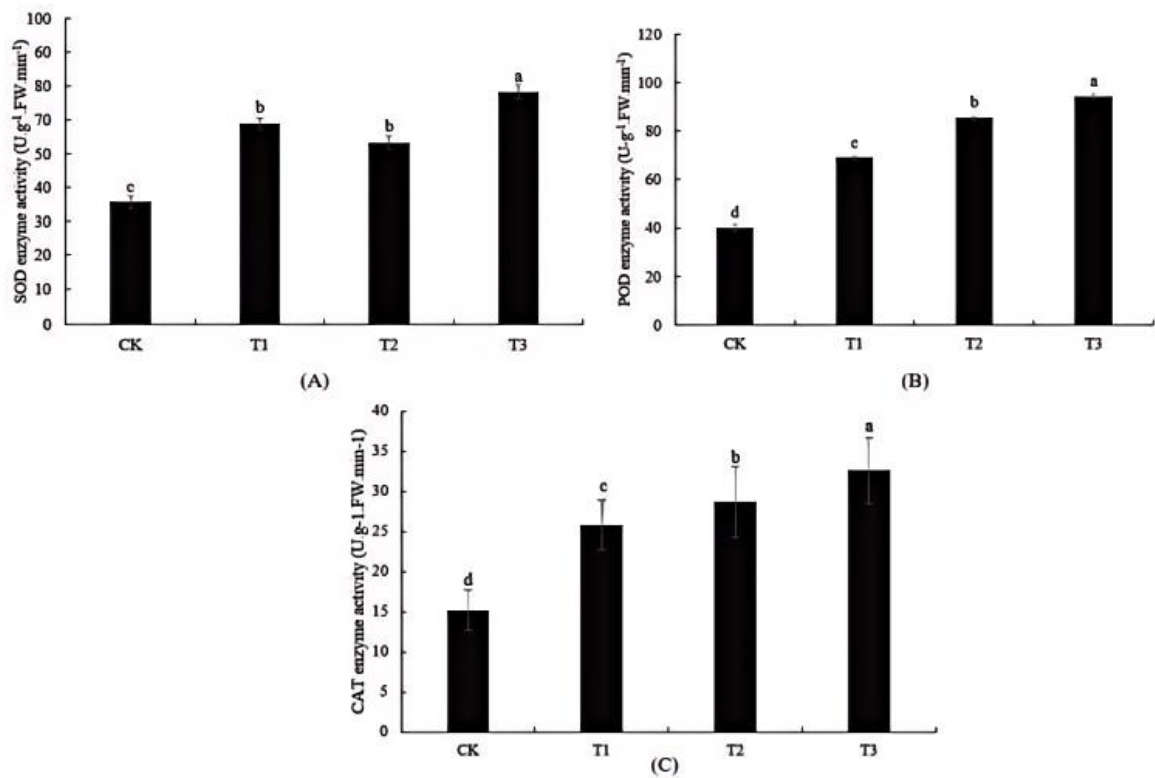


Figure 7 Changes of chlorophyll contents in seedling leaves under the treatments with

different concentrations of LaCl₃

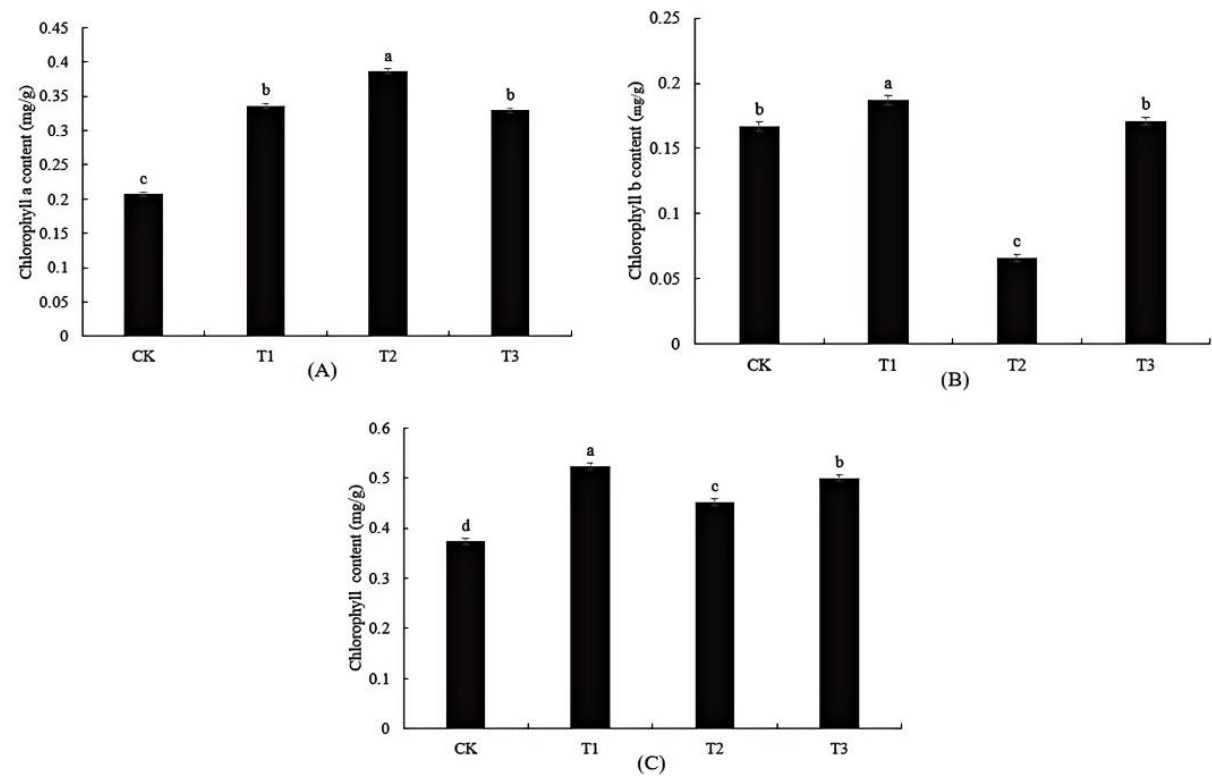


Table 1 Correlation between physiological and biochemical indexes and other factors during germination of wheat treated with different concentrations of LaCl₃

Metric	M±SD	Seedling height	Germination rate of seeds	Fibrous root number	Seedling root length
SOD activity	43.5±6.02	0.214	-0.690	-0.849	-0.900
POD activity	72.2±22.0	-0.389	-0.802	-0.988*	-0.976*
CAT activity	25.6±7.1	-0.446	-0.774	-0.940	-0.950
Chlorophyll content	0.462±0.058	-0.171	-0.394	-0.967*	-0.887

Note: The results of the hypothesis test of the Pearson correlation coefficient corresponding to the asterisk annotation system: Single Star (*) marked $P < 0.05$ significance threshold, double star (**) marked $P < 0.01$ extremely significant level, both using two-sided probability test. M ± SD indicates Mean ± Standard Deviation of the data.