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Effects of cadmium stress on the growth and physiological characteristics of sweet potato

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Abstract

This study evaluated the responses of sweet potatoes to Cadmium (Cd) stress through pot experiments to theoretically substantiate their comprehensive applications in Cd-polluted agricultural land. The experiments included a CK treatment and three Cd stress treatments with 3, 30, and 150 mg/kg concentrations, respectively. We analyzed specified indicators of sweet potato at different growth periods, such as the individual plant growth, photosynthesis, antioxidant capacity, and carbohydrate Cd accumulation distribution. On this basis, the characteristics of the plant carbon metabolism in response to Cd stress throughout the growth cycle were explored. The results showed that T2 and T3 treatments inhibited the vine growth, leaf area expansion, stem diameter elongation, and tuberous root growth of sweet potato; notably, T3 treatment significantly increased the number of sweet potato branches. Under Cd stress, the synthesis of chlorophyll in sweet potato was significantly suppressed, and the Rubisco activity experienced significant reductions. With the increasing Cd concentration, the function of PS II was also affected. The soluble sugar content underwent no significant change in low Cd concentration treatments. In contrast, it decreased significantly under high Cd concentrations. Additionally, the tuberous root starch content decreased significantly with the increase in Cd concentration. Throughout the plant growth, the activity levels of catalase, peroxidase, and superoxide dismutase increased significantly in T2 and T3 treatments. By comparison, the superoxide dismutase activity in T1 treatment was significantly lower than that of CK. With the increasing application of Cd, its accumulation accordingly increased in various sweet potato organs. The the highest bioconcentration factor was detected in absorbing roots, while the tuberous roots had a lower bioconcentration factor and Cd accumulation. Moreover, the transfer factor from stem to petiole was the highest of the potato organs. These results demonstrated that sweet potatoes had a high Cd tolerance and a restoration potential for Cd-contaminated farmland.

Keywords Sweet potato, Cd stress, Carbon and nitrogen metabolism, Antioxidant enzyme system, Repair potential

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Introduction

Cadmium (Cd) is a non-essential and highly toxic heavy metal, which causes prevalent soil pollution in countries and is regarded as a global environmental concern [1, 2]. Cd enrichment in soils can be attributed to various factors, such as geological weathering, mining and smelting activities, industrial emission, automotive emission, wastewater irrigation, and agricultural production processes [3–5]. With extremely high water solubility and a long half-life, soil Cd can be absorbed by plants and enters the human diet through the food chain, with 50–70% of the absorption by kidneys and liver, greatly threatening human life and health [6–8]. At present, soil Cd pollution remediation technologies mainly include physical remediation (excavating, filling, permafrost remediation, etc.), chemical curing (such as chemical extraction), and bioremediation [9]. Phytoremediation removes heavy metals from the soil in situ using various plants and is considered a cost-effective remediation measure, which is superior to traditional physical and chemical remediation methods [10].

As a major food crop worldwide, sweet potato (*Ipomoea batatas*) quality and yield have received wide attention, and improving its output value and production safety has been identified as an important measure to promote rural economic development [11]. Sweet potato is well-suited for the safe utilization of Cd-polluted cultivated land. Its large aboveground biomass facilitates Cd transfer from the soil and enrichment, ensuring the safety of edible parts. In addition, the skin of its underground roots effectively blocks horizontal Cd transfer, contributing to wide applications in several paddy fields with heavy Cd pollution (soil total Cd content of 1.0–2.0 mg/kg) [12]. When exposed to Cd stress, plants experience symptoms such as slow leaf growth, yellowing, and reduced leaf area. The chlorophyll structure and synthesis are affected, and the activity levels of key photosynthesis enzymes are reduced. Additionally, the expression of genes related to photosynthesis is downregulated, thereby affecting plant photosynthesis and growth [13–17]. Cadmium stress led to changes in the absorption and transport efficiency of nutrients by plants, resulting in abnormal metabolic processes, morphological alterations, and nutrient deficiencies in plants [18]. This inhibition of nutritional balance in plants by cadmium arises from its competition with essential metal transporters and displacement of other essential elements from molecular binding sites [19]. According to the research conducted by Quan Zhang and colleagues, cadmium stress disrupted the homeostasis of various nutrients to varying degrees, with the most significant decreases observed in iron and manganese levels [20].

In addition, Cd-induced oxidative stress disrupts the cell membrane and intracellular osmotic equilibrium, which is maintained by crucial substances, such as soluble sugar and fructose [21, 22]. Oxidative stress is also an important physiological indicator of a plant's response to Cd stress. Cd may indirectly promote the production of reactive oxygen species (ROS) by destroying the chloroplasts in leaves and inactivate various enzymes by directly binding to the specific sites, thus disrupting the ROS balance. In this sense, the production of ROS by oxidative stress is one of the first metabolic changes observed in Cd-exposed plants [23]. Regulation of antioxidant enzymes can provide plants with additional protection against oxidative stress, and cadmium stress produces plasma membrane-bound NADPH oxidase in peroxisomes of rice and pea plants and leads to the production of reactive oxygen species [24].Ruilian Sun et al. demonstrated that cadmium stress significantly increased windflower leaf superoxide dismutase activity, root peroxidase activity, and leaf and root catalase activity [25]. When plants are subjected to Cd stress, symptoms such as slow growth, greenish coloration, and reduction of leaf area occur, which not only affects the structure and synthesis of chlorophyll, but also reduces the activities of key enzymes in photosynthesis, and inhibits the expression of genes related to photosynthesis, thus affecting plant photosynthesis and growth and development [26]. Under Cd stress, the activities of the key enzymes of photosynthesis are affected, and the synthesis of chlorophyll and carotenoids is inhibited, and chlorophyll a/b/c and chlorophyll a/b/c are inhibited, and chlorophyll a/b/c are inhibited. inhibition, and down-regulation of chlorophyll a/b binding protein. Heavy metals such as Cd significantly reduced net photosynthetic rate, transpiration rate, stomatal conductance and intercellular carbon dioxide concentration. In addition, Cd stress reduced the maximum photochemical efficiency (Fv/Fm), potential activity (Fv/Fo), actual photochemical efficiency of PSII (ΦPSII), and photochemical burst coefficient (qP) of leaves by 4.0% [27].

Most plant roots absorb Cd and enrich it in a bound state in the epidermis, cell wall, and cortical cells, while the content of intracellular Cd^{2+} is small and mainly concentrated in the vacuole and nucleus [28]. Understanding the molecular mechanisms of the regulatory network of plant Cd tolerance is an important way to protect plants from Cd stress and a prerequisite for human health and food safety. It has been reported that Cd transport and sensing can activate signaling cascade responses in plants and that Cd-induced signaling correlates with exogenous and endogenous levels of plant growth regulators [29]. According to the research conducted by Li and colleagues, some key genes (including transcription factor family genes) could be targeted to improve Cd tolerance in Hibiscus sabdariffa under high Cd treatment, and the up-regulated genes in the MYB, NAC, AP2/ERF, and

WRKY families may play a key role in the regulatory network of Cd stress tolerance in Hibiscus sabdariffa [30]. Aiguo Yin and his team employed transcriptome analysis methods to uncover the molecular mechanisms underlying differential cadmium (Cd) accumulation in two sweet potato varieties, identifying a number of crucial differentially expressed genes (DEGs), including *PDR*, *HMA3*, *COPT5*, *CAX3*, *GAUT*, *CCR*, *AUX1*, *CAT*, *SOD*, *GSR*, and *GST*. These DEGs were found to be involved in pathways such as heavy metal transport or detoxification, cell wall biosynthesis, plant hormone signal transduction, and glutathione metabolism [31]. Research conducted by Wu and his colleagues demonstrated that the heterologous expression of the *BcIRT1* and *BcZIP2* genes from Pak Choi (*Brassica chinensis* L.) in yeast enhanced the sensitivity of various yeast mutant strains to metal ion (Cd^{2+}, Mn^{2+}) stress, facilitating the accumulation of heavy metal ions within the yeast cells [32].

Cd enters the edible parts of the plant from the root through apoplast pathways, and subcellular localization studies found that most of this element is taken up by the root system from the apoplast [33]. The high pectin content and strong pectin methyl esterase activity in plant roots enhance the Cd interception ability of the cell wall and convert Cd in the root system into inert forms, thus reducing the harm of Cd stress on plants [34, 35]. The research results on the Cd accumulation differences of 14 sweet potato varieties showed differences in the Cd accumulation of different sweet potato varieties. However, most varieties exhibited small differneces in Cd concentration variation trends in various tissues of the same plant, ranked as aboveground part > roots > tuberous root skin > tuberous root flesh [36].

Approximately 20 million hectares of cultivated land in China have been contaminated with metals to varying degrees, with cadmium being one of the primary pollutants [37]. Guizhou Province is a typical cadmium geochemical anomaly area, that means Cadmium content in soil is 144% higher than the average cadmium content in cultivated land in China [38]. The inherent high cadmium content in the soil poses a severe environmental constraint on the sustainable development of agriculture in Guizhou. Sweet potato, an important crop for food, feed, and economic purposes, was the focus of this experiment, which involved subjecting it to different concentrations of cadmium stress in a pot-cultured setting. The study aimed to investigate the effects of varying cadmium levels in soil on the carbon metabolism, dry matter accumulation and distribution, as well as yield formation of sweet potato. Furthermore, it explored the migration and accumulation patterns of cadmium within the soil-sweet potato system. The ultimate goal was to preliminarily understand the response mechanisms of sweet potato to multiple cadmium stresses, thereby providing theoretical support for safe sweet potato production and soil environmental remediation in areas with high cadmium backgrounds.

Methods

Materials and growth conditions

The pot experiments were conducted in the greenhouse of the teaching test site of Guizhou University in 2021. The *Ziyun* red sweet potato (virus-free seedlings) provided by Anshun Academy of Agricultural Sciences was tested. The pot measures 39.5 cm in height, 64 cm in top diameter, and 30 cm in bottom diameter. Each pot was filled with 75 kg of air-dried soil screened through a 4 mm sieve. Then, the sieved soil was mixed with 0.2 g/kg of nitrogen (N) (urea), 0.15 g/kg of phosphorus (calcium superphosphate), and 0.3 g/kg of potassium (potassium sulfate) as a one-time application of base fertilizers. The basic physical and chemical properties of the tested soil are as follows: pH = 6.25, organic matter content = 2.69 g/kg, total *N* = 0.86 g/kg, alkaline hydrolysis *N* = 87.00 mg/kg, total phosphorus = 0.94 g/kg, rapidly available phosphorus (P_2O_5) = 89.15 mg/kg, total potassium = 7.6 mg/kg, rapidly available potassium (K_2O) = 114.1 mg/kg, and soil Cd content = 0.27 mg/kg. The seedlings were transplanted on May 27, 2021. Before transplantation, the soil clumps in pots were crushed with a gardening shovel and stirred uniformly. Seedlings with consistent growth were selected and washed to remove the rhizosphere substrate and then transplanted in pots, each containing three seedlings. Root-fixing water was applied according to the maximum moisture content of the soil. After the recovering stage, the seedlings were grown in the greenhouse, and the water management was based on the field moisture capacity of 60–70%. No fertilizer was applied to the surface of the topsoil. The other management measures were consistent with typical field cultivation.

Test methods

On March 27, 2021, the maximum moisture content of the soil was calculated. Solutions containing different Cd contents were prepared using $3CdSO_4 \cdot 8H_2O$ and poured into the corresponding pots at one time. In contrast, an equal amount of distilled water was added into the CK pot. The pots were placed in the greenhouse (25 °C, 60% humidity) for two months. A single-factor randomized block design was adopted, with four Cd concentrations of 0 mg/kg (CK), 3 mg/kg (T1), 30 mg/kg (T2), and 150 mg/kg (T3). The substrate soil used in this pot experiment had a cadmium background value of 0.27 mg/kg, which was lower than the safe soil cadmium level of 0.3 mg/kg stipulated by the industry standards for the production of environmentally-friendly foods in China [39]. Therefore, this soil was selected as the test substrate. The experimental setup with a cadmium stress concentration of

3 mg/kg was based on the European Union's limit standard for cadmium content in soil, which is set at 3 mg/kg [40]. The reason for setting a stress concentration of 30 mg/kg in the experiment was as follows: Relevant studies have shown that sweet potatoes maintain a high growth potential even under a cadmium stress concentration of 20 mg/kg, indicating that sweet potatoes exhibit high tolerance to this level of cadmium stress [41]. To delve deeper into the response mechanism of sweet potatoes to cadmium, this experiment, building upon previous research, increased the cadmium stress concentration and designed a treatment at 30 mg/kg. The reason for setting a stress concentration of 150 mg/kg in the experiment was as follows: Due to high geological backgrounds which mean Cadmium content is high in this geology and the exploitation and smelting of mineral resources, Guizhou Province suffers from severe heavy metal contamination in its soil, with some contaminated areas having cadmium levels exceeding 150 mg/kg. In order to further explore the potential of sweet potatoes in remediating locally contaminated heavy metal soils, this experiment included a treatment with cadmium at 150 mg/kg [42]. Three replicates were established for each treatment group, totaling 48 pots. Samples were harvested at four growth periods of sweet potatoes after transplantation in the greenhouse, i.e., the seedling stage P1 (30 d after transplanting), the initial growth stage P2 (60 d after transplanting), the stage of rapid growth of tuberous root P3 (90 d after transplanting), and the harvest stage P4 (120 d after transplanting). Samples were collected from three pots of each treatment. Specifically, two individual plants were used for dry matter measurements. The net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), intercellular carbon dioxide concentration (Ci), SOD, POD, CAT activity, 1,5-bisphosphate ribulose carboxylase activity, fluorescence parameters, chloroplast pigments, and leaf area were measured in the 4th-6th functional leaf; the indexes such as the uptake of Cd for transporter accumulation were carried out by organs, and the organs were leaves, petioles, stems, tubers, and roots (fiber roots, burdock roots). The collected samples were placed in sample boxes and transported to the lab at low temperatures. Subsequently, they were rinsed with distilled water and stored in a refrigerator at -80 °C for later use.

Determination of agronomic traits, dry matter accumulation, and yield

Indicator measurements and sampling were performed on sweet potato plants in the P1, P2, P3, and P4 periods, corresponding to 30, 60, 90, and 120 d after transplantation. When sampling for dry matter measurements, the whole plant was placed in the sample box, transported to the lab at a low temperature, rinsed with distilled water, and wiped clean with gauze. The length of the longest sweet potato vine was measured with a tape measure, the mesurement of stem diameter was conducted using a vernier caliper, and the leaf area per plant was gauged with a LI-3100 C benchtop leaf area meter; The fresh weight of root, stem, leaf, petiole, and tuberous root was determined. After de-greening process, these parts were dried to a constant weight and weighted. Finally, the dry samples were prepared after grinding and sieving through a 100-mesh nylon screen. Upon harvesting, the underground tuberous root yield was taken the standard value by calculating the average yield of the three replicates in each treatment.

Determination of cd content and cd-related parameters

Specifically, 0.5 g of dry sample needs to br accurately weighted. To this end, the plant samples were passed through a 100 mesh sieve, placed in the microwave digestion tank. Then, 6 ml HNO_3 (superior purity) and 2 ml H_2O_2 (superior purity) were added. Subsequently, the samples were placed at room temperature for 12 h and digested in the microwave digestion instrument at 180 °C for 2 h. After cooling down, the acid volume was reduced to about 1 mL, and 3% dilute HNO_3 (superior purity) was incorporated to the concentrated acid, resulting in 20 mL of the final solution The heavy metal Cd content in the solution was determined using ICP-MS [43, 44].

The Cd transport factor (TF) of different organs was calculated. This indicator can quantify the ability of the plant to transfer metals from the underground to the aboveground parts. For example, TF(stem/root)=stem Cd concentration/root Cd concentration.The Cd bioconcentration factor (BCF) of different organs was calculated: BCF=tissue Cd concentration/soil Cd concentration [45].

Determination of photosynthetic characteristic indicators

Chloroplast pigments were extracted using 95% ethanol. The chlorophyll *a* and chlorophyll *b* contents were determined using UV-Vis spectrophotometer at 665 nm and 649 nm according to the specific absorbance values [46].

The PAM-2500 portable modulated chlorophyll fluorometer was used to assess chlorophyll fluorescence. Leaves were subjected to dark adaptation using dark-adapted fixture for 30 min. The functional leaf, i.e., the fourth unfolded leaf top from the shoot tip, was measured. The minimum fluorescence under dark-adaptation (Fo), maximum fluorescence under dark-adaptation (Fm), minimum fluorescence under light-adaptation (Fo′), maximum fluorescence under light-adaptation (Fm′), and steady state fluorescence under light-adaptation (Fs) were dertermined. The Fo′, Fm′, and Fs measurements were repeated three times. The fluorescence yield was calculated. The potential photosystem II photochemical

quantum efficiency can be calculated according to Fv/Fm = (Fm-Fo)/Fm; The expression for computing the photochemical quenching coefficient is qP= (Fm′-Fs)/(Fm′-Fo′); The non-photochemical quenching can be obtained, as NPQ = (Fm-Fm′)/Fm [47, 48].

Based on the survey of agronomic traits in sweet potato, representative plants were harvested at seedling, early growth, bloom, and harvest stages after transplantation from 9:00 a.m. to 11:00 a.m. on a sunny day. After sampling, the net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and interstitial carbon dioxide concentration (Ci) of the top 4–5 unfolded leaves of the plants were measured with the LI-6400 photosynthesis tester. The operation parameters of the instrument were: CO_2 concentration of 400 μmol·mol^{-1}, light intensity of 1500 μmol·m^{-2}·s^{-1}, ambient relative humidity of 40–80%, and ambient temperature at 25 °C [49].

The Ribulose 1,5-bisphosphate carboxylase activity was determined using the assay kit (Suzhou Keming Biotechnology Co., Ltd., Suzhou, China) in strict accordance with the instruction manual.

Assay of antioxidant enzyme activity

The activity of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) was determined using the same enzyme activity kits aforementioned.

Determination of carbohydrates

The soluble sugar content was detected using the anthrone sulfate method. In addition, the 3,5-dinitrosalicylic acid method was adopted for starch content measurement [50].

Data statistics and analysis

In this study, IBM SPSS Statistics 23 was used to analyze the significance of LSD differences. We also implemented Microsoft Excel 2010 for data statistics and tabulation. Data visualization was performed in Origin 2022. GraphPad Prism (Version: Prism 9) was applied to draw the histograms and analyze the significance, and the resulting images were integrated using Adobe Illustrator (Version: 2023).

Results

Effects of cd stress on sweet potato growth

To explore the effects of Cd stress on sweet potato growth, we analyzed various growth indicators under different treatments throughout the experimental period of interest. The results showed that a lower Cd concentration (T1) significantly promoted the vine growth of sweet potato during the P1 stage. With increasing Cd concentrations (T2, T3), the increase in stem diameter, vine length, and leaf area in the middle and late growth stages were inhibited more pronounced. In particular, the T3 treatment delivered significant inhibitory effects on the sweet potato stem diameter enlargement at P4 stage (Fig. 1A), Stem diameter of T3 treatment at P4 was 17.18% lower than CK; the vine length elongation at P2 and P3 stages (Fig. 1B), and the leaf area expansion at P2–P4 stages (Fig. 1D). In addition, the number of sweet potato branches in the P2 stage was also significantly inhibited under T1 and T3 treatments. In contrast, sweet potato branches in the late growth stages experienced significant growth in number under the T3 treatment (Fig. 1C). at P4, the number of branches was 35.77% higher in T3 treatment than CK.

Compared to CK, the sweet potato dry matter weight decreased more significantly with the increase in Cd concentration (Fig. 1E). In particular, T2 and T3 treatments significantly reduced the dry matter weight throughout the whole growth period, At P4, the dry matter mass of T3 treatment was 45.22% lower than CK.

Effects of cd stress on sweet potato antioxidant enzyme system

During the whole sweet potato growth period, the leaf POD, CAT, and SOD activity increased significantly with the rising Cd concentration. With the application of three Cd concentrations, the leaf POD activity was significantly higher than that of CK, except for the insignificant effect in the P2 stage under the T2 treatment (Fig. 2A). The leaf CAT activity was most significantly affected under T2 and T3 treatments (Fig. 2B). When the plant further grew, the leaf SOD activity underwent an initial increase, followed by a decrease, and then an increase, and the T1 treatment significantly reduced the SOD activity in the late growth period. In contrast, T3 treatment significantly enhanced the leaf SOD activity in most of the growth periods except for the P3 stage (Fig. 2C), At P4, SOD enzyme activity of T3 treatment was 39.23% higher than CK.

Effects of cd stress on sweet potato carbon metabolism

Throughout the sweet potato growth period, leaf Pn, Gs, and Tr showed decreasing trends with the increase in Cd concentration. In contrast, leaf Ci experienced significant increases. In particular, T2 and T3 treatments significantly reduced the sweet potato leaf Pn at various stages of the growth period compared to CK (Fig. 3A), At P4 period, Pn of T1 treatment was 19.14% lower than CK treatment; Pn of T2 treatment was 22.03% lower than CK treatment; Pn of T3 treatment was 36.84% lower than CK treatment. T3 treatment significantly suppressed the Gs, Tr, and Ci during early growth. In the late growth period, the increased Cd concentration increased sweet potato leaf Ci and insignificantly inhibited Gs and Tr (Fig. 3B and C, and 3D).

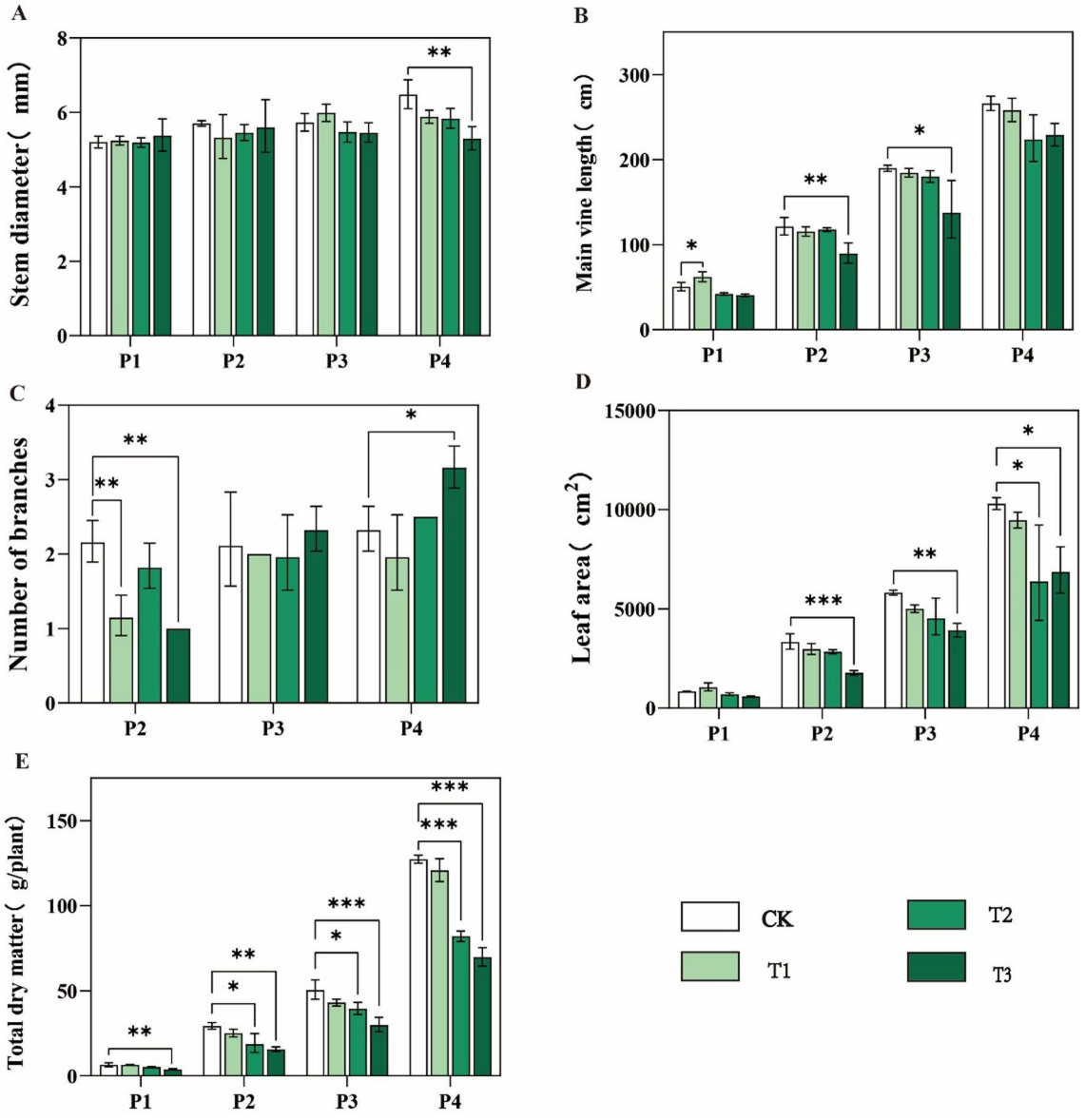

Fig. 1 Effects of Cd stress on sweet potato growth indexes. **A**: Stem thickness; **B**: Vine length; **C**: Number of branches; **D**: Leaf area; **E**: Dry matter mass. Different asterisks indicate significant differences ($p < 0.05$) between different Cd treatments, with one asterisk (*) indicating a 0.05 significance level, two asterisks (* *) representing a 0.01 significance level, and three asterisks (* * *) corresponding to a 0.001 significance level. P1–P4 respectively represent the seedling stage (transplanted for 30 d), the initial growth stage (transplanted for 60 d), the prosperous growth stage (transplanted for 90 d), and the harvest stage (transplanted for 120 d). Different shades of green indicate the concentration gradient of Cd stress. Four Cd treatments with various concentrations comprise the CK (0 mg/kg), T1 (3 mg/kg), T2 (30 mg/kg), and T3 (150 mg/kg). The caption for the following figure is the same as this

During the growth period, the functional leaf RuBP activity first increased and then decreased, peaking in the prosperous growth stage. Compared with CK, leaf RuBP activity during P1 period was significantly reduced with elevating Cd concentration. In P2 and P4 stages, T1 treatment promoted the RuBP activity in leaves with rises in Cd concentrations, while T2 and T3 treatments exhibited the opposite effects; in P3 period, the RuBP activity experienced significant decreases in T2 and T3 treatments, and this decline was not significant under T1 treatment (Fig. 4A), During the P3 period, RuBP activity of T2 treatment was 36.30% lower than CK; RuBP activity of T3 treatment was 44.74% lower than CK.

It was indicated that T1 treatment did not influence sweet potato leaf NPQ, qP, and Fv/Fm. In contrast, the T2 and T3 treatments had more significant effects. Notably, T3 significantly increased the sweet potato leaf NPQ compared to CK in the early stage of sweet potato growth and induced significant reductions in the P4 stage (Fig. 4B), NPQ of T3 treatment was 36.30% lower than CK. In addition, T3 treatment significantly reduced the sweet potato leaf qP in the P1, P2, and P4 stages (Fig. 4C).

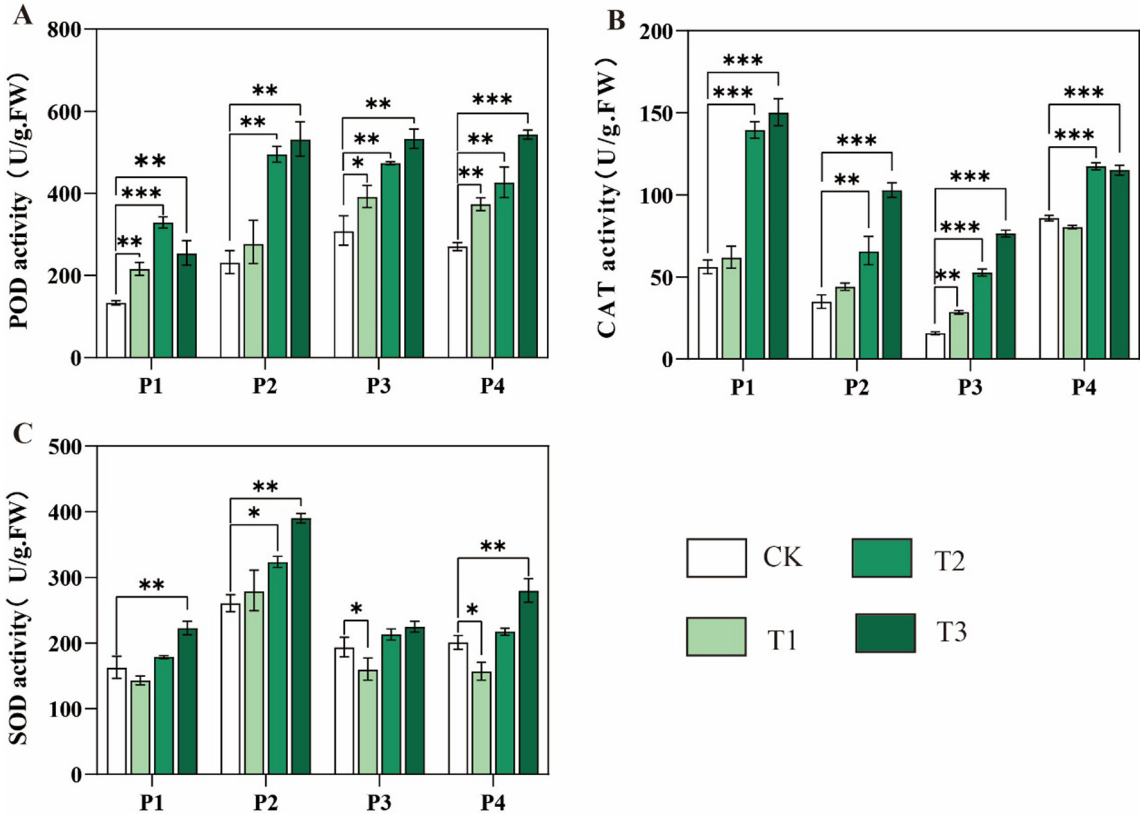

Fig. 2 Effect of Cd stress on oxidase activities in functional leaves of sweet potato. **A**: POD activity; **B**:CAT activity; **C**: SOD activity

Similarly, T2 treatment reduced sweet potato NPQ and qP in the P4 stage. Notably, the Cd stress had no significant effects on sweet potato NPQ and qP in the P3 stage (Fig. 4B and C). The sweet potato leaf Fv/Fm values were lower than those in CK under Cd treatments, especially T3 treatment, which led to significant decreases in the P1, P3, and P4 stages (Fig. 4D), During P1, Fv/Fm of T3 treatment was 8.75% lower than CK; During P3, Fv/Fm of T3 treatment was 10.0% lower than CK; During P4, Fv/Fm of T3 treatment was 6.17% lower than CK;

Total chlorophyll content showed a decreasing trend under Cd treatment and showed significant or highly significant differences between treatment and control with increasing stress concentration. Chlorophyll a/b, P1 period, was not significantly different from CK at low concentration, but the ratio was significantly higher at medium concentration of stress and 12.25% higher at high concentration than CK. At P2, P3, and P4 after treatment, the overall trend of cadmium stress leading to different degrees of elevation of the ratio was demonstrated, with the absolute values of the range of the magnitude of change in P2, P3, and P4 ranging from 12.14 to 13.08%, 4.10–0.91%, 7.42% to 12.87 (Fig. 4E and F).

Effects of cd stress on sweet potato yield and quality

With the increase in soil Cd concentration, the individual plant sweet potato weight showed a decreasing trend, Significant differences were reached among the treatments, and the fresh weight of single plant in T1 treatment was 17.34% lower than that of CK, T2 treatment was 62.79% lower than that of CK, T3 treatment was 79.63% lower than that of CK (Fig. 5A). In the harvest stage, the sweet potato tuberous root starch content decreased with the rising Cd concentration, and the difference between treatments and CK was significant, starch content in T1 treatment was 18.73% lower than that of CK, T2 treatment was 18.15% lower than that of CK, T3 treatment was 16.97% lower than that of CK (Fig. 5B). During the harvest period, as the Cd concentration increases, the content of soluble sugars in sweet potato tubers showed an increasing trend. Significant differences were achieved among the treatments (Fig. 5C).

Sweet potato cd absorption, transport, and accumulation characteristics

Throughout the sweet potato growth period, the petiole-stem Cd TF was the largest among the plant organs of interest. The BCFs of various sweet potato organs showed decreasing trends with the increase in Cd concentration. In addition, the largest BCF was the largest

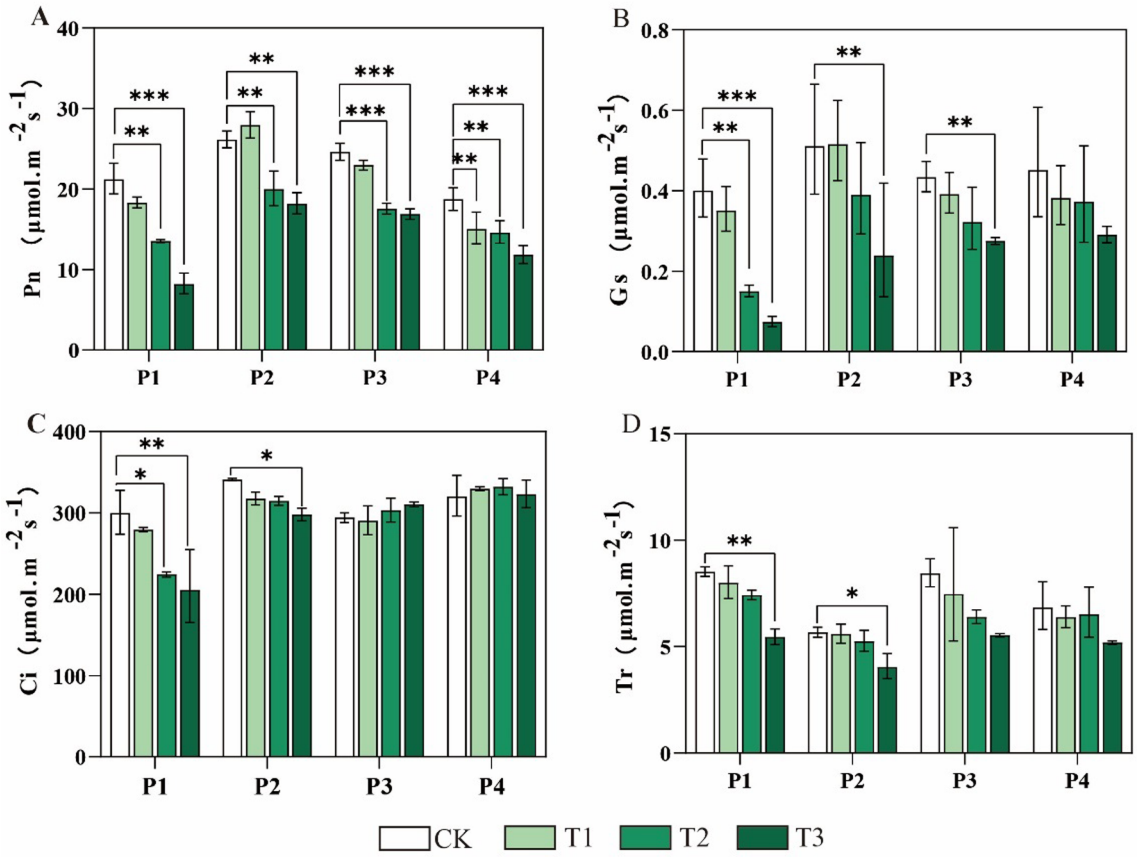

Fig. 3 Effect of Cd stress on photosynthetic parameters. **A**: net photosynthetic rate (Pn); **B**: stomatal conductance (Gs); **C**: intercellular carbon dioxide concentration(Ci); **D** transpiration rate (Tr)

in the root and the smallest in the leaves throughout the growth period. In the harvest stage, the Cd TFs of various sweet potato organs ranked as follows: TF (petiole-stem) > TF (leaf-stem) > TF (tuberous root-root) and TF (leaf-root) (Fig. 6A). The sequence of BCFs in various sweet potato organs were BCF (root) > BCF (stem) > BCF (petiole) > BCF (tuberous root) > BCF (leaf) (Fig. 6B).

According to Table 1, the Cd contents in sweet potato roots, stems, leaves, petioles, and tubers increased with rising Cd concentration and reached the maximum values under T3 treatment. The Cd contents in these organs showed significant differences among treatments. In the P1 stage, the highest accumulation concentrations of Cd were found in roots, followed by leaves and stems. In the P2 stage, the Cd contents in the roots, stems, and petioles treated with T1 decreased by 25.94%, 17.85%, and 43.05%, respectively, compared to the seedling stage; the corresponding Cd contents in T2 treatment decreased by 33.27%, 8.15%, and 12.05%, respectively, compared to the P1 period; in addition, the Cd contents in T3 roots, stems, leaves, and petioles dropped by 9.09%, 17.62%, 11.89%, and 12.40%, respectively, compared to the P1 period. Compared to P2 stage, during the P3 period, the Cd contents in sweet potato roots and leaves in T1 group experienced 25.87% and 16.22% reductions, respectively; the Cd contents in the roots, stems, leaves, and petioles in the T2 group decreased by 36.55%, 30.63%, 16.67%, and 10.85%, respectively; in addition, the Cd content in the mentioned four organs in the T3 group underwent 31.94%, 9.07%, 4.19%, and 22.78% decreases, respectively. During the P4 period, T1 treatment exhibited 16.87% and 54.86% decreases in the Cd contents in sweet potato roots and tubers respectively, compared to the P3 period; the relative reductions in Cd content in the roots, stems, leaves, petioles, and tubers in T2 were 10.35%, 8.65%, 6.66%, 18.57%, and 54.99% respectively; moreover, in the case of T3 treatment, the relative Cd content in the potato roots, stems, petioles, and tubers decreased by 6.35%, 19.06%, 12.58%, and 58.52%, respectively.

Comprehensive analysis of sweet potato indicators under cd stress

As shown in Fig. 7, Gs, Ci, and Tr had no significant correlation with the Cd concentrations of sweet potato tuberous roots, leaves, and absorbing roots. In contrast, these parameters were significantly correlated with the indicators, such as Fv/Fo, qP, RuBP, Pn, chlorophyll, POD, SOD, vine length, and yield. Among them, the Cd

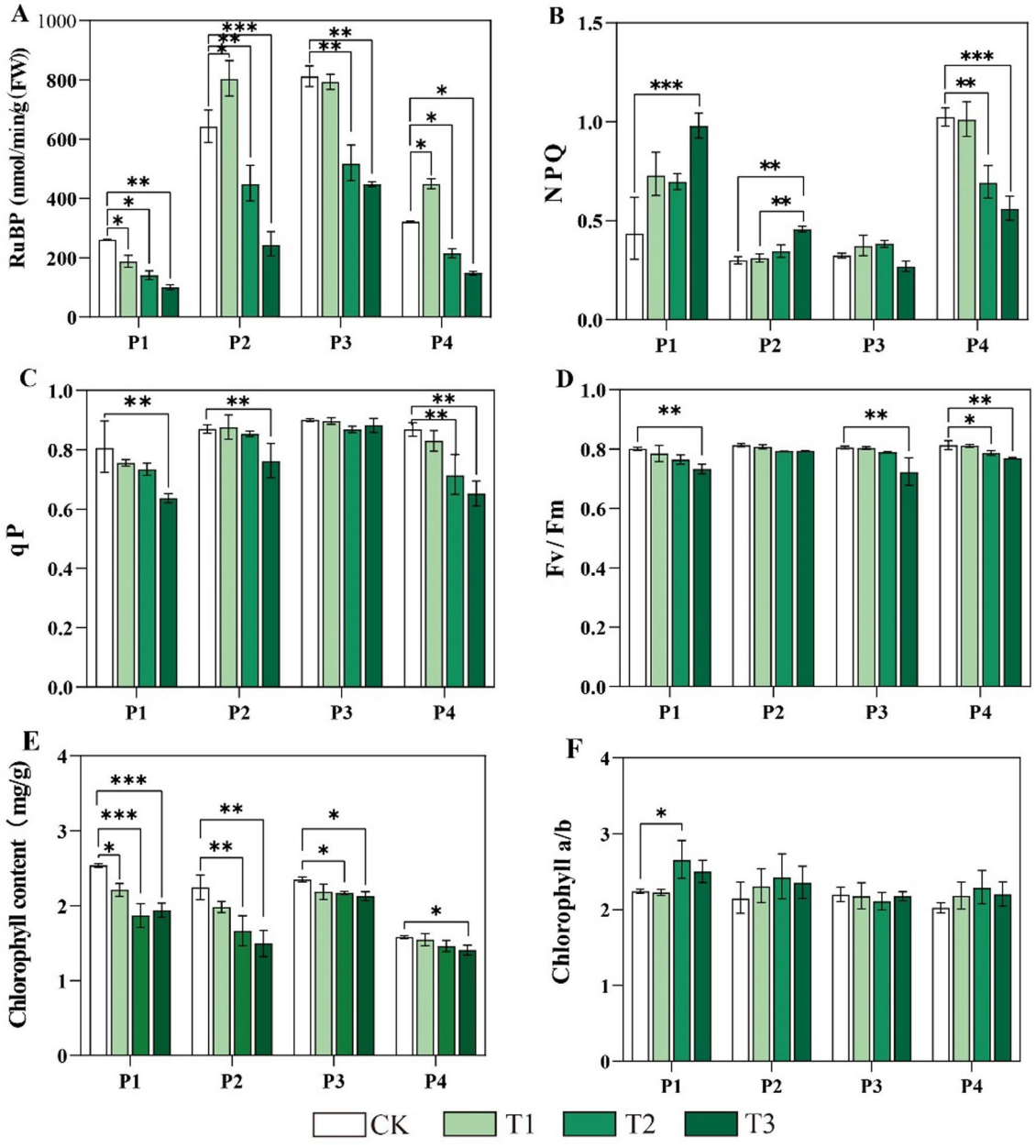

Fig. 4 Effect of Cd stress on fluorescence parameters in sweet potato. **A**: RuBP activity(RuBP); **B**: Non-photochemical quenching coefficient (NPQ) ; **C**: Photochemical quenching coefficient(qP); **D**: Maximum quantum efficiency of PSII(Fv/Fm); E:Total chlorophyll content(chlorophyll content); F:chlorophyll *a*/*b*(Chlorophyll a/b)

concentrations of sweet potato tuberous roots, leaves, and absorbing roots were significantly positively correlated with the activity of POD and SOD.

Discussion

As a non-essential metal element, Cd accumulation in plant organs negatively affects necessary physiological processes and plant growth [51, 52]. Cd toxicity impairs plant growth, and increased Cd concentrations significantly inhibit plant growth, manifested by the yellowing and bifurcation of plants and the stunted growth of stems and roots [53]. Long-term Cd stress leads to plant root necrosis, decomposition, and mucification, thereby inhibiting the elongation of roots and buds, leading to leaf curling and yellowing [54]. This study found that Cd stress significantly increased the number of sweet potato branches, and the effect under high Cd concentrations was more significantly than other treatments in the harvest stage. The reason may be that the accumulation of Cd in sweet potato stems destroys the apical meristematic tissues of the stems, leading to a decrease in apical dominance and an increase in the number of branches.

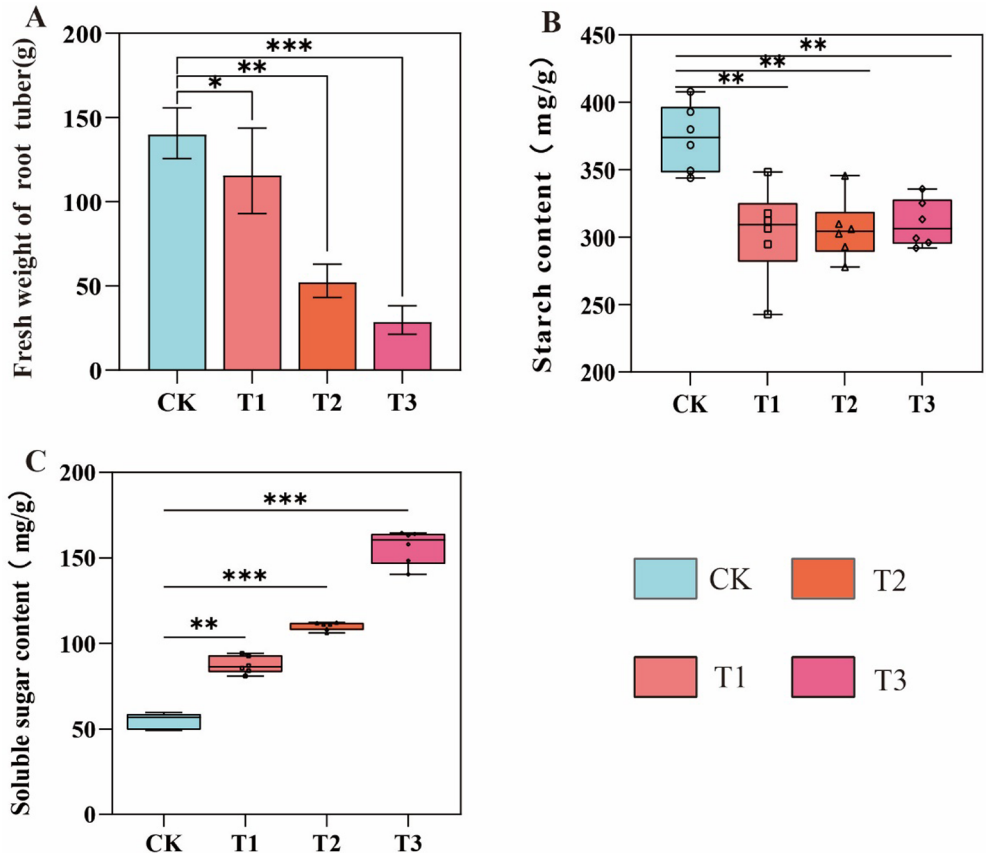

Fig. 5 Effect of Cd stress on sweet potato yield and quality. **A**: Individual potato weight (Fresh weight); **B**: Starch content; **C**: Soluble sugar content

However, the number of leaves and the leaf area under high Cd concentrations were significantly lower than those under CK and low Cd concentrations. Cadmium enrichment may affect the physiological activity at the stem-petiole junction, causing damage to the lower end of the petiole and leading to leaf abscission.

Sugar metabolism also plays an important role in plant growth and stress response. Sucrose, glucose, fructose, and other soluble sugars can act as signaling molecules regulating gene expression and osmotic protectants for biomolecules and membranes [55]. The reed stem starch content increased under Cd stress, indicating the ability of starch to bind to Cd in the reed stem to reduce the aboveground Cd concentration [56]. In this study, the starch content of sweet potato tuberous roots showed a decreasing trend with the increase in soil Cd concentration, and the CK treatment demonstrated a significantly higher content than that under other Cd treatments. Low Cd concentrations had no significant effect on the soluble sugar content of various sweet potato organs, while higher Cd concentrations exhibited significant increases in the plant organs. From these findings, it is hypothesized that sweet potato becomes more tolerant to Cd during growth, thus mitigating the effect of Cd on soluble sugar content.

Photosynthesis is the foundation of crop growth and a key factor in plant yield. Under Cd stress, sweet potato photosynthesis was inhibited, significantly reducing its growth. Chlorophyll is an important pigment involved in the absorption, transmission, and transformation of light energy during photosynthesis, and its content is important for plant growth. Under Cd stress, the chlorophyll contents are reduced in crops such as maize, barley, tomato, and mustard [57–60]. The experimental results in this article showed that under Cd stress, the total chlorophyll content of sweet potato was significantly lower than that of CK. Specifically, the Chlorophyll *a*/*b* content was reduced during P3 stage and increased during the rest of the growth cycle. Cd also reduces the absorption of nutrients such as manganese, iron, and magnesium, and increasing intracellular Cd concentrations interfere with the insertion of Mg^{2+} into protoporphyrins or replace Mg^{2+} in chlorophyll *a* and *b* to destruct chlorophyll structure [61]. When stomatal limits predominate, intercellular carbon dioxide, transpiration rate, and net photosynthetic rate decrease synchronously. In contrast, when non-stomatal limits predominate, the transpiration rate and net photosynthetic rate decrease while the intercellular carbon dioxide concentration increases. The reason is that non-stomatal limiting factors hinder CO_2

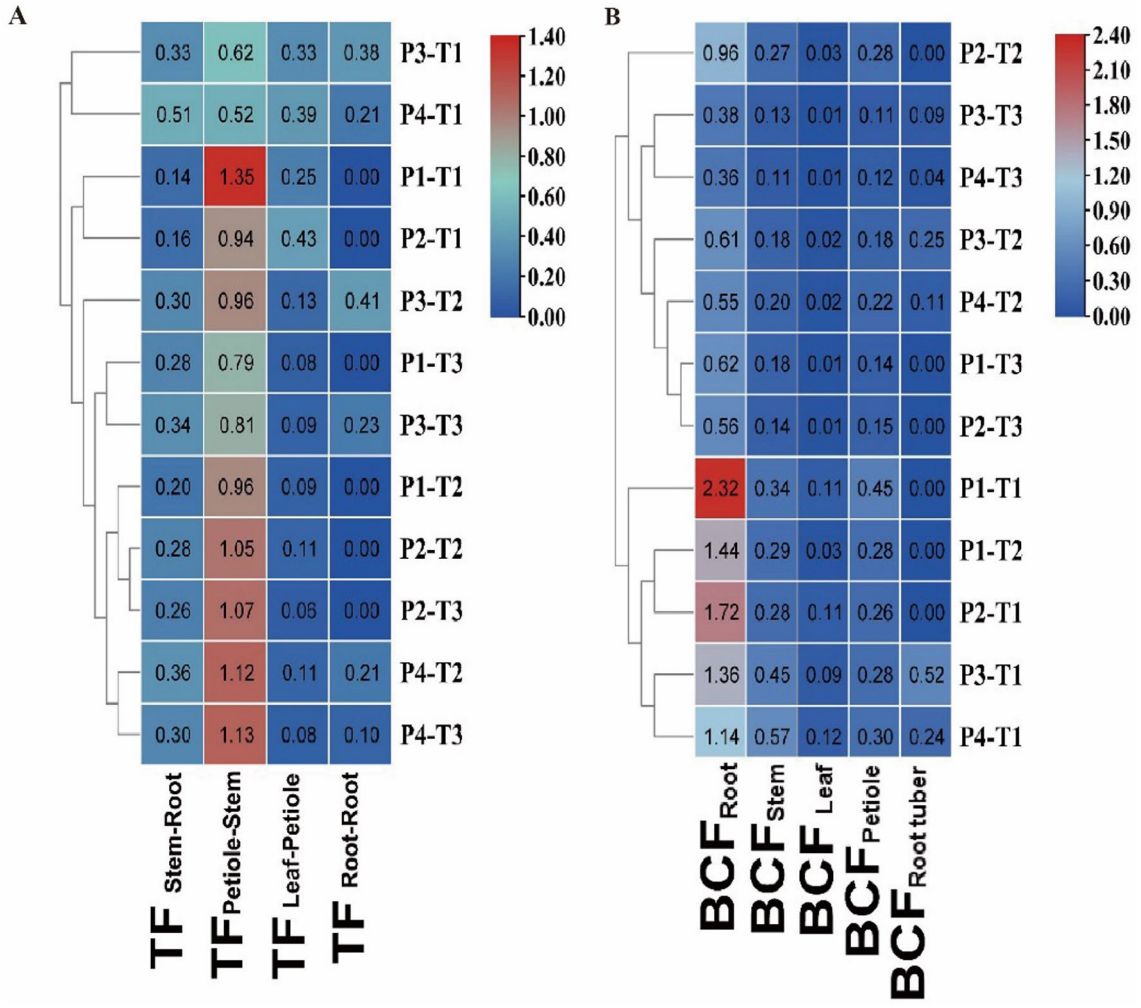

Fig. 6 Characteristics of Cd uptake-transfer accumulation in sweet potato. **A**: Cd transfer coefficient(TF); **B**: Cd enrichment coefficient(BCF)

Table 1 Cadmium content characteristics of sweet potato organs in different periods

Period	Treatment	Cadmium content (mg/kg)				
		Roots	Stems	Leaves	Petioles	Root tubers
P1	CK	0.37 ± 0.06d	0.26 ± 0.01c	0.16 ± 0.01d	0.22 ± 0.03c	
	T1	7.75 ± 0.17c	1.12 ± 0.11c	0.38 ± 0.01c	1.51 ± 0.19c	
	T2	43.37 ± 1.68b	8.71 ± 0.84b	0.76 ± 0.04b	8.38 ± 0.36b	
	T3	89.75 ± 3.24a	25.43 ± 1.22a	1.6 ± 0.1a	20.00 ± 1.12a	
P2	CK	0.43 ± 0.01c	0.34 ± 0.02c	0.21 ± 0.01d	0.16 ± 0.02c	
	T1	5.74 ± 0.08c	0.92 ± 0.04c	0.37 ± 0.01c	0.86 ± 0.04c	
	T2	28.94 ± 2.65b	8.00 ± 0.35b	0.9 ± 0.03b	7.37 ± 0.59b	
	T3	81.59 ± 6.52a	20.95 ± 1.27a	1.43 ± 0.07a	22.48 ± 1.74a	
P3	CK	0.28 ± 0.02c	0.36 ± 0.01c	0.13 ± 0.01c	0.16 ± 0.01c	0.027 ± 0.03d
	T1	4.56 ± 0.17c	1.51 ± 0.12c	0.31 ± 0.03c	0.93 ± 0.02c	1.75 ± 0.22c
	T2	18.36 ± 0.81b	5.55 ± 0.27b	0.75 ± 0.06b	6.57 ± 0.28b	7.62 ± 0.7b
	T3	55.53 ± 3.18a	19.05 ± 1.21a	1.37 ± 0.12a	17.36 ± 0.86a	12.61 ± 0.36a
P4	CK	0.37 ± 0.08c	0.26 ± 0.01d	0.14 ± 0.01c	0.11 ± 0.01c	0.025 ± 0.01d
	T1	3.79 ± 0.2c	1.91 ± 0.09c	0.39 ± 0.03c	0.99 ± 0.05c	0.79 ± 0.06c
	T2	16.46 ± 0.61b	5.07 ± 0.36b	0.70 ± 0.03b	5.35 ± 0.23b	3.43 ± 0.25b
	T3	52 ± 2.86a	15.42 ± 0.53a	1.37 ± 0.09a	15.42 ± 1.43a	5.23 ± 0.32a

Different letters indicate significant differences between samples ($P < 0.05$)

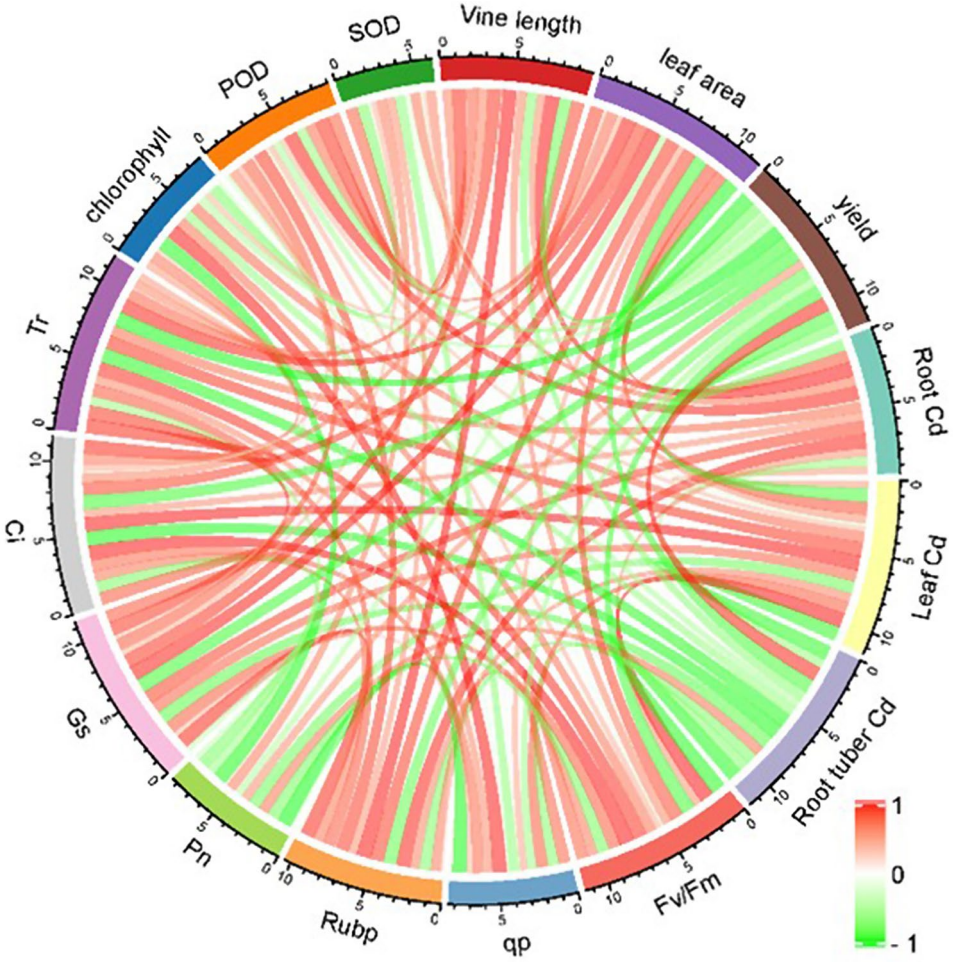

Fig. 7 Comprehensive analysis between indicators of Cd stress on sweet potato. The red band represents positive correlation, the green band represents negative correlation, the darker the color, the greater the correlation (positive or negative correlation), and the wider the band, the larger the absolute value

fixation, resulting in CO_2 accumulation in the intercellular space [62].The net photosynthetic rate, stomatal conductance, and transpiration rate of sweet potato leaves showed a decreasing trend with increasing Cd concentration. By comparison, the intercellular carbon dioxide concentration decreased with the concentration rise in the P1 and P2 periods while increased in the P3 and P4 periods. Based on these observations, it was indicated that the decreased photosynthesis under Cd stress was attributed to the stomatal limits in the first two stages of the sweet potato growth period, and non-stomatal limits caused increases in the latter two stages. The test results showed that with the increase in Cd concentration, the sweet potato leaf Fv/Fm and qP exhibited a decreasing trend, and NPQ exhibited a significant increasing trend. Therefore, with the increase of Cd concentration, the PSII reaction center excitation energy capture efficiency of sweet potato leaves decreased, the PSII; function was affected, and the PSII activity and openness were reduced. As a result, the light energy utilization was decreased, primarily contributing to decline in photosynthetic capacity of sweet potato leaves.

To reduce the effects under stress, non-enzymatic and enzymatic antioxidant protection systems in plants are typically activated to remove ROS. Rice and pea plants under Cd stress can produce plasma-membrane binding NADPH oxidase in peroxisomes, thereby producing ROS. Cd may also indirectly promote the production of ROS by destroying chloroplasts in leaves. Cd toxicity also stimulates the development of ROS in the mitochondrial electron transfer chain [24]. The results of this experiment showed that Cd stress significantly increased the peroxide scavenging enzyme activity in sweet potato plants. In addition, significant differences in POD content were found between CK and treatments. CAT contents were also significantly different between CK group and Cd groups with medium and high concentrations. This disparity indicated that Cd stress produced substantial ROS in sweet potato, and the concentration of ROS was correlated with the intensity of stress. This observation

is consistent with the findings of Mahnoor Asif, Ismat Nawaz et al. [63, 64]. In addition, Cd also significantly inhibited the enzymatic activity of SOD and CAT in sunflowers, common beans, and peas [65]. The activities of GPX and APX in wheat and maize were increased under Cd stress, and the activity of POD in rape was minimized [66]. Based on the above analysis, a diagram of the pattern of sweet potato response to Cd stress is produced .When Cd^{2+} enters sweet potato through root-related transporter proteins and plastid pathway [67], it has some effects on agronomic and physiological traits of sweet potato. Leaf area, vine length, chlorophyll content, qP, Fv/Fm, yield, and RuBP activity of sweet potato under Cd stress decreased, and CAT, POD, and SOD enzyme activities were elevated (Fig. 8).

Plant roots are the main parts providing water and nutrients, and the root hairs can regulate root penetration and accelerate ion infiltration [68]. Under Cd stress, the root hair density of *Arabidopsis thaliana* is positively correlated with the Cd^{2+} concentration in the plant, indicating that the root hair is the most active for absorbing Cd^{2+} [69]. In Arabidopsis, both the Fe(II) transporter IRT1 and the Mn transporter Nramp1 can participate in Cd absorption [70]. Studies have shown that the translocation of Cd from roots to shoots is influenced by factors such as xylem loading capacity, vacuolar sequestration of Cd, and the duration of Cd retention in the apoplastic space. Once transported to the shoots, Cd is further distributed to different tissues and organs [71]. This indicated that *BcIRT1* and *BcZIP2* possess the capability to transport cadmium ions in Pak Choi. The *OsNARAMP* gene family in rice (*Oryza sativa* L.), responsible for the transport of divalent or trivalent cations, consisted of at least seven members in the past. Specifically, *OsNARAMP1* was localized on the plasma membrane of plant cells. Overexpression of *OsNARAMP1* led to increased accumulation and translocation of cadmium (Cd) in rice leaves, suggesting that *OsNARAMP1* may play a significant role in the accumulation of cadmium in the aerial parts of rice [72]. Cd absorbed by the root system enters the stem through the transporter protein OsHMA2, which is the key to the Cd transfer from root to stem [1]. The results of this study showed that with the increase in soil Cd concentration, the ranking of Cd TFs in various organs was: TF (petiole/stem) > TF (stem/root) > TF (tuber/root) > TF (leaf/petiole). The BCFs generally ranked as BCF (root/ground) > BCF (stem/ground) and BCF (petiole/ground) > BCF (tuberous root/ground) > BCF (leaf/ground). The BCF (root/ground) was greater than 1 in some treatments, while the BCFs of all other treatments were less than 1, indicating that the root was the main Cd bioconcentration site of sweet potato. During the tuberous root-to-stem transport, some Cd was fixed in the root system, consistent with the findings of Pan et al. on *Canna indica* Cd stress resistance [73]. In the upward transfer of Cd, the petiole and stem were also the main Cd storage sites of sweet potatoes and were involved in reducing the Cd accumulation in the leaves. The findings of previous studies were largely consistent with those of this research, revealing that under

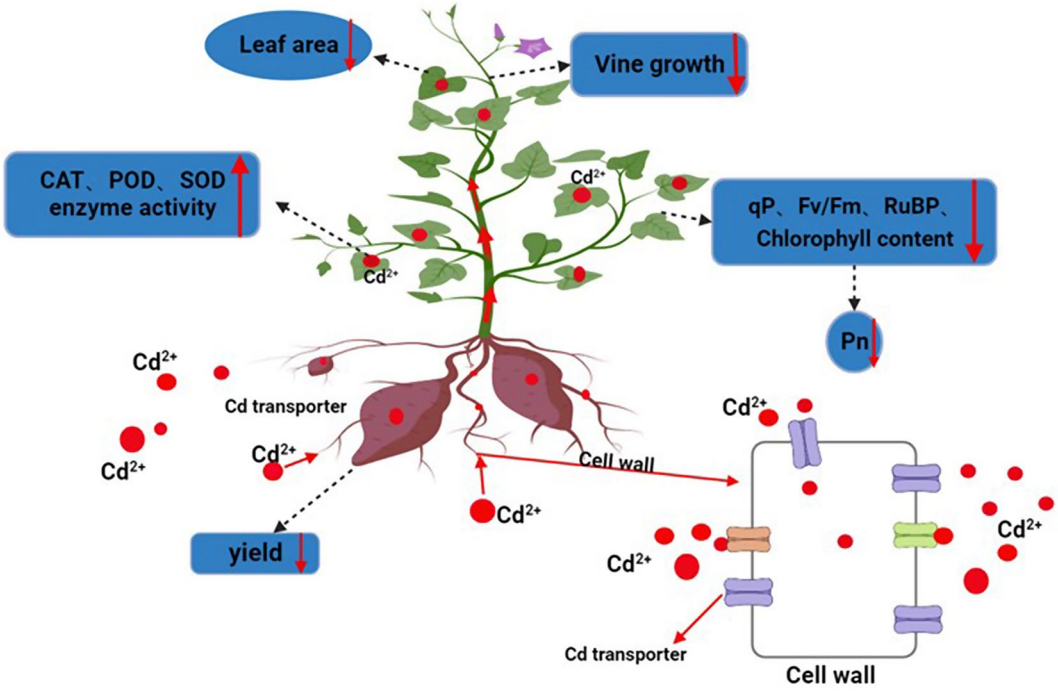

Fig. 8 Patterns of sweet potato in response to Cd stress

a relatively high cadmium soil background, sweet potatoes still exhibited robust growth. Quantitative analysis of cadmium accumulation in various organs indicated that traditional economic organs of sweet potatoes also had relatively low cadmium enrichment coefficients. Our study demonstrated that at a soil cadmium content of 3 mg/kg, a common phenomenon in Guizhou Province, sweet potatoes retained their value for human and animal consumption and processing. At around 30 mg/kg, sweet potatoes were suitable for forage but required careful selection of parts. Tuberous roots were not recommended for fresh consumption or food processing but could be utilized for energy production and other non-food purposes. In the range of approximately 150 mg/kg, we solely recommended using sweet potatoes as phytoremediators for cadmium-contaminated soil, as they temporarily lacked the value for biological food consumption. Given the prevalent high cadmium background in Guizhou's soil, we suggest making adjustments in the selection of edible aboveground parts, preferably opting for sweet potato leaf tissues. In light of cadmium's high mobility, it is imperative to strengthen dynamic monitoring of cadmium-contaminated soil and continuously screen for low-accumulation and cadmium-tolerant sweet potato varieties. Complementary agronomic measures should be implemented to reduce cadmium accumulation, thereby ensuring food safety and revitalizing the countryside.

Conclusions

This study found that under medium and high Cd concentrations, the sweet potato vine length, leaf area, and stem diameter were inhibited, the individual plant dry matter weight was decreased, and the number of branches was increased. Cd stress suppressed chlorophyll synthesis and significantly reduced the activity of Rubisco, a key enzyme for photosynthesis. Additionally, the sweet potato leaf Fv/Fm and qP showed decreasing trends, and NPQ exhibited a significant increase. With the increase in Cd concentration, the activity of all three antioxidant enzymes in sweet potato leaves was increased. In addition, the Cd accumulation and transport differed in varioust organs under Cd stress, with the highest BCF in the root and the highest TF from the stem to the petiole. The results of this study showed that sweet potatoes had a high Cd tolerance. This suggests high comprehensive utilization value of this crop for Cd-polluted cultivated lands.

This work has limitations. (1) Considering a variety of soils in nature, using a unified soil Cd content threshold as the evaluation standard for ecological agricultural products may result in pronounced errors. (2) The exogenous addition of inorganic Cd salts in this experiment increased Cd effectiveness. Notably, differences exist in the total Cd threshold between potted and natural soil environments, potentially influencing the assessment of sweet potato Cd environmental remediation capacity. Next research plans are summarized as follows: (1) It is recommended to conduct point-to-point sampling of sweet potato soil in the field production system. (2) Cd stress studies on sweet potato varieties can consider different production areas and types. The relevant research results have practical value in promoting green and high-quality production of sweet potatoes and guiding the safe utilization of polluted farmland.

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Author contributions

Conceptualization, T.R. and S.T.; methodology, S.T.,G.C.; software, T.R.,R.X.; validation, T.R., L.X. and R.X. ; formal analysis, T.R.; investigation, T.R., L.X., Y.L.,P.W.,Y.Q.,X.Z.; resources, S.T.; data curation, T.R.; writing—original draft preparation, T.R.; writing—review and editing, T.R.; visualization, T.R.,S.T.; supervision, S.T.,G.C.; project administration, S.T.; funding acquisition, S.T. All authors have read and agreed to the published version of the manuscript.

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Data availability

Data is provided within the manuscript or supplementary information files.All processed data and data graphs can be obtained from the first author(1947298252@qq.com).

Declarations

Competing interests

The authors declare no competing interests.

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