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Research Article

Effect of silicon addition on the growth and photosynthesis of *Castanopsis hystrix* in manganese stress

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Abstract

Silicon (Si) plays important role in reducing the toxic effects of manganese (Mn) in plants, however, more research is needed to elucidate the photosynthetic response with different Si and Mn treatments. This study aimed to investigate the alleviating effect of Si on the growth and photosynthesis of *Castanopsis hystrix* (*C. hystrix*) under Mn stress. Seedlings were grown in pot experiments with five Mn levels (0, 200, 600, 1500, and 3000 $mg \cdot kg^{-1}$) and four Si levels (0, 115, 230, and 460 $mg \cdot kg^{-1}$). The results showed that three types of (positive, stagnant, and negative) growth of *C. hystrix* seedlings were observed among twenty treatments. Low concentrations of Si ($Si \leq 115\ mg \cdot kg^{-1}$) and Mn treatments ($Mn \leq 600\ mg \cdot kg^{-1}$) can stimulate a positive growth of seedlings by increasing net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs). The 230 $mg \cdot kg^{-1}$ Si with low concentration of Mn treatments can cause a stagnant growth of seedlings by increasing Gs, Tr and maximum photochemical efficiency of PSII (Fv/Fm) but decreasing intercellular carbon dioxide concentration (Ci). High concentrations of Si ($Si \geq 460\ mg \cdot kg^{-1}$) or Mn treatments ($Mn \geq 1500\ mg \cdot kg^{-1}$) treatments can cause negative growth of seedlings by decreasing photochemical quenching (qP), non-photochemical quenching (qN), Gs, Pn and pigment contents. The application of Si alleviated the stress induced by Mn and promoted the growth-defense regulation mechanism of seedlings to avoid stress. Hence, we concluded that the most suitable concentration of Si was 115 $mg \cdot kg^{-1}$ Si for *C. hystrix*'s growth under low Mn stress.

Keywords: *Castanopsis hystrix*; positive growth; Si alleviation; photosynthetic response; Mn stress

Introduction

Twentieth-century soil heavy metal pollution has become a significant environmental issue that not only affects food production safety and anthropogenic health but also causes environmental and atmospheric

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pollution (Briffa *et al*., 2020). Heavy metals are defined as chemical elements with an atomic density above 5 $g{\cdot}cm^{-3}$ and an atomic number greater than 20, and those elements must exhibit metallic properties (Raychaudhuri *et al*., 2021). Numerous heavy metals, such as zinc (Zn), manganese (Mn), and cobalt (Co), are essential for living organisms, but only trace amounts are required (Xu *et al*., 2022). The accumulation of heavy metals in soils is highly correlated with soil fertility, anthropogenic activities, production, biodiversity, plant metabolism, and the health of biological organisms (Li *et al*., 2023). Soil heavy metal pollution is primarily found in industrial and mining cities, posing a significant challenge to local ecosystems (FAO, 2021). Excessive accumulation of heavy metals can lead to serious impacts, such as water quality degradation, vegetation destruction, and threats to organisms (FAO, 2021; Briffa et al., 2020). Soil heavy metal pollution is widespread and severe in China, making it urgent to implement more appropriate soil remediation methods to remediate the contaminated soils (Qin *et al*., 2021).

Mn, as one of the most abundant metals on earth, plays a crucial role in the biogeochemical cycle of carbon (C), nitrogen (N), sulfur (S), and iron (Fe) (Tebo *et al*., 2005). The amount of Mn in soils varies greatly, with the world's average Mn content in soil being 850 $mg{\cdot}kg^{-1}$, but in some areas, the soil Mn content can be dozens to hundreds of times higher than the average level (Chen *et al*., 2023). Most studies have shown that anthropogenic activity, such as mining operations, industrial waste, manganese fertilizers, and pesticides, contribute to the increasing in soil Mn pollution (Machado *et al*., 2020; Vargas *et al*., 2022). Trace amounts of Mn are beneficial for improving the biosynthesis and metabolism process of plants, but excessive accumulation of Mn in tissues can lead to Mn toxicity and even reduce growth and productivity (Stohs and Bagchi, 1995; Hauck *et al*., 2003; Socha and Guerinot, 2014; Vatansever *et al*., 2017). The toxic effects of Mn on plants can vary widely among different species (Mora *et al*., 2009; Yang *et al*., 2019). Silicon (Si), another abundant elements, has been found to have beneficial effects on plant growth and productivity, particularly under stressful environment (Emamverdian *et al*., 2018). Si has been shown to increase plant height, seed weight, total root length and improve the quality of several crop plants, such as rice, wheat, maize, and soybean (Adrees *et al*., 2015; Rethore *et al*., 2020). Therefore, Si is considered a beneficial element for plant species that helps regulate plant growth and reduce abiotic and biotic stresses (de Oliveira Rocha *et al*., 2022). Another important characteristic of Si is its ability to alleviate Mn toxicity, as reported by numerous researchers (Bolan *et al*., 2011; Ma and Yamaji, 2006). However, the analysis of the interaction between Mn and Si and the alleviating effect of Si on Mn stress in woody plants still requires further investigation. Additionally, there are few studies on the ability of Si to alleviate high doses of Mn stress on woody plants.

Woody plants, known for their long growth time, abundant biomass and deep roots, have a greater potential to restore ecological function and mitigate environmental degeneration (Capuana, 2011). *Castanopsis hystrix* (*C. hystrix*), a native and precious economic tree species with a well-developed root system, is a fast-growing afforestation tree species that has high potential for carbon storage in China (Li *et al*., 2023). It has gained more attention due to its ecological, economic and social value, including carbon storage, environmental greening, and global warming mitigating (Li *et al*., 2023). Natural forests of *C. hystrix* are widely distributed in southern China, including Guangxi, Guangdong, Yunnan, and Fujian, and their planted areas continue to increase annually (Liu and Xu, 2021). The Mn content in top soils ranges from 40 $mg{\cdot}kg^{-1}$ to 11,546 $mg{\cdot}kg^{-1}$ in southern China, highlighting the urgent need to address Mn pollution caused by mining and industrial activities (Qin *et al*., 2021; Liang and Teng, 2021). Previous studies have indicated that *C. hystrix* adapts well to Mn-polluted soils (Shi *et al*., 2023). However, current research on *C. hystrix* focuses on gene diversity, plant tissue culture, and plantation technique, with a lack of studies on the regulatory mechanism of Si on *C. hystrix* growth and photosynthesis under different Mn toxicity (Li *et al*., 2023). Therefore, we conducted pot experiments to investigate the influence of Si addition on *C. hystrix* growth, biomass, pigments, photosynthetic index, and chlorophyll fluorescence under different Mn stress. We hypothesize that low doses of Si may be effective in alleviating Mn stress, while the high doses of Si may not alleviate Mn stress. This study will give more valuable information on the adaptation mechanism of *C. hystrix* seedlings, providing a theoretical reference for the proper utilization of Si of *C. hystrix* seedlings in Mn-polluted soils.

Materials and Methods

Experimental design

This study was conducted in the experimental area of the forestry college of Guangxi University, China (108°17′9.00″E, 22°50′28.41″N). The area has a subtropical monsoon climate with abundant sunlight and precipitation. The mean annual temperature is 21.7 °C, the mean annual precipitation is 1304.2 mm, and the mean relative humidity is 79%. Six-month healthy and uniform seedlings of *C. hystrix* (Height: 35.55 ± 4.43 cm, basal diameter: 4.26 ± 1.05 mm) were collected from the Guangxi Forestry Research Institute, which serves as the national *C. hystrix* propagation research and cultivation base in China. The soil was collected from a *C. hystrix* forest near Nanning, Guangxi province, where soil collapsed due to rainfall. The soil was transported to the experimental site, air-dried at 20-35 ℃ for two months, ground, sieved (1 cm), and thoroughly mixed to ensure uniform physical properties (Wu *et al.*, 2021). The soil had a yellowish-red color, and the physical-chemical properties were as follows: pH 5.2, organic matter 27.13 $g \cdot kg^{-1}$, total nitrogen 0.67 $g \cdot kg^{-1}$, total phosphorus 0.16 $g \cdot kg^{-1}$, total potassium 14.99 $g \cdot kg^{-1}$, ammonium nitrogen 5.62 $mg \cdot kg^{-1}$, nitrate nitrogen 4.71 $mg \cdot kg^{-1}$, available phosphorus 4.9 $mg \cdot kg^{-1}$, and available potassium 27.14 $mg \cdot kg^{-1}$.

Previous planting experiments have shown that 5 kg of dried soils in a 25 cm × 22 cm pot can sustain normal growth for *C. hystrix* seedlings within a year (Liang and Teng, 2021; Liu and Xu, 2021). Therefore, 5 kg of air-dried soil were placed into plastic grow bags (25 cm in height and 22 cm in diameter). The pot experiment was conducted using a completely randomized design (CRD) with ten replicates. A total of twenty treatments were designed in Table 1. On July 5th, 2020, seedlings were planted in plastic grow bags and left to stabilize for one month. Each pot was irrigated 100 mL of water per day to keep a 60-70% of field capacity. One month later, five Mn levels (0, 200, 600, 1500, and 3000 $mg \cdot kg^{-1}$) were developed with manganese sulfate ($MnSO_4 \cdot H_2O$) solution and four Si levels (0, 115, 230, and 460 $mg \cdot kg^{-1}$) were developed with sodium silicate ($Na_2SiO_3 \cdot 9H_2O$). Five concentrations of Manganese sulfate solution ($MnSO_4 \cdot H_2O$ concentration: 0, 5.12, 15.36, 38.41, and 76.82 $g \cdot L^{-1}$) were watered six times (on August 5, August 15, August 25, September 5, September 15 and September 25, 2020) respectively, 100 ml per basin at a time. Four concentrations of Sodium silicate solution ($Na_2SiO_3 \cdot 9H_2O$ concentration: 0, 14.54, 29.07, and 58.14 $g \cdot L^{-1}$) were watered four times (on October 25, November 1, November 8, and November 15, 2020) respectively, 100 ml per basin at a time. The seedlings were harvested four months later.

Table 1. The concentration of different Mn and Si treatments

Mn element ($mg \cdot kg^{-1}$) **Si element ($mg \cdot kg^{-1}$)**	**0 (Mn0)**	**200 (Mn200)**	**600 (Mn600)**	**1500 (Mn1500)**	**3000 (Mn3000)**
0 (Si0)	Si0Mn0(CK)	Si0Mn200	Si0Mn600	Si0Mn1500	Si0Mn3000
115 (Si115)	Si115Mn0	Si115Mn200	Si115Mn600	Si115Mn1500	Si115Mn3000
230 (Si230)	Si230Mn0	Si230Mn200	Si230Mn600	Si230Mn1500	Si230Mn3000
460 (Si460)	Si460Mn0	Si460Mn200	Si460Mn600	Si460Mn1500	Si460Mn3000

Measurements of photosynthetic pigments

The content of chlorophyll a (Chl a), chlorophyll b (Chl b), chlorophyll a+b (Chl a+b), and carotenoids (Car) was measured using the approach of Lichtenthaler (1987). The topmost mature leaves were collected and 0.1 g of fresh leaves were chopped and dipped overnight in a mixture of acetone, absolute ethanol and distilled water ($V_{acetone}$ / $V_{ethanol}$ / $V_{absolute\ distilled\ water}$ = 4.5:4.5:1) for the extraction of photosynthetic pigments.

Then, the supernatant was centrifuged at 4,000 rpm for 10-15 minutes. Using the spectrophotometer (Thermo BioMate 3, USA), absorbance values of supernatant were measured under wavelengths of 665, 649, and 470 nm, respectively. Pigment content was measured using the following formulas:

$$\text{Chl a (mg/L)} = 13.95\times A665-6.88\times A649 \quad (1)$$
$$\text{Chl b (mg/L)} = 24.96\times A649-7.32\times A665 \quad (2)$$
$$\text{Chl a+b (mg/L)} = \text{Chl a}+\text{Chl b} \quad (3)$$
$$\text{Car (mg/L)} = (1000\times A470-2.05\times \text{Chl a}-114.8\times \text{Chl b})/245 \quad (4)$$

Where the A665, A649, and A470 are absorbance at 665, 649, and 470 nm wavelengths. Then, the content of photosynthetic pigments was calculated as mg· g^{-1} fresh weight.

Photosynthetic index and chlorophyll fluorescence parameters

Photosynthetic indexes, including the net photosynthetic rate (Pn), transpiration rate (Tr), intercellular carbon dioxide concentration (Ci), and stomatal conductance (Gs), were measured three times before harvesting using a portable infrared gas analyzer (LI-6400XT, USA). Measurements were done on the topmost fully expanded mature leaves on a sunny and cloudless morning (08:30-11:30 am).

Chlorophyll fluorescence parameters, including the maximum photochemical efficiency of PSII (Fv/Fm), efficient quantum yield of PSII (Y(II)), photochemical quenching (qP), non-photochemical quenching (qN), and linear rate of photosynthetic electron transport (ETR), were determined using a portable pulse modulated fluorometer (Hanse TechFMS-2, UK). Prior to measurements, the plant was dark-adapted for one hour. Measurements were done on the same topmost fully expanded mature leaves on a sunny and cloudless night (08:00-12:00 pm).

Plant growth and biomass

The *C. hystrix* seedlings were divided into roots, stems, and leaves. The roots were firstly washed with tap water and then with distilled water to remove soil, ions and dust. Then, the filter paper was used to absorb the water from the surface of each tissue. For the measurements of dry weight, *C. hystrix* tissues were oven-dried at 105 °C for 30 min and then at 70 °C for 48-72 hours until a constant weight was achieved (Wu *et al.*, 2021). The dry weight of roots, stems, and leaves was recorded, and the total biomass was calculated as the sum of the biomass of each tissue.

Data analysis

All values reported in this experiment are means ± standard errors (SE) (n=3). To compare the effects of different Si and Mn treatments on plant growth and photosynthesis, the two-way analysis of variance (ANOVA) followed by Duncan's new multiple-range test was conducted in "stats" packages in R. The significance level was set at $P < 0.05$. Besides, the hierarchical cluster method was used to classify the types of plant growth among twenty treatments. Redundancy analysis (RDA) was used to estimate the relationship between photosynthesis and plant growth in each clustering result, and hierarchical partitioning was further used to assess the importance of photosynthetic indicators in plant growth (Lai *et al.*, 2022). All figures were visualized in "ggplot2" packages in R 4.0.0, the hierarchical cluster, RDA and hierarchical partitioning was conducted in "MASS", "vegan", and "rdacca.hp" packages, respectively, in R 4.0.0 (R Core Team, 2023).

Results

Plant growth in different Si and Mn treatments

Results from Table 2 and Figure 1 showed that the Si, Mn, and Si × Mn interaction treatments significantly influenced the growth of *C. hystrix* seedlings ($P < 0.05$). In the absence of Mn treatment, the aboveground (stem and leaf) biomass and total biomass firstly increased with the addition of 115 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn200 treatment, the aboveground biomass decreased with the increasing Si concentration, while the total biomass firstly increased with the addition of 115 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn600 treatment, the aboveground biomass decreased with the increasing Si concentration, while the root biomass and total biomass firstly increased with the addition of 115 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn1500 and Mn3000, the biomass of *C. hystrix* seedlings decreased with the increasing Si concentration. In the absence of Si or in the presence of Si460 treatment, the aboveground biomass and total biomass decreased with the increasing Mn concentration, while the root biomass firstly increased with the addition of 200 and 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. In the presence of Si 115 and Si230 treatment, the root biomass and total biomass firstly increased with the addition of 600 mg·kg^{-1} Mn and then significantly decreased with the increasing Mn concentration. Furthermore, the highest promoting effect on aboveground biomass and total biomass was observed at the concentration of 115 mg·kg^{-1} Si and 200 mg·kg^{-1} Mn, which were 28.3~33.3%, 17.0~23.9%, and 21.5~29.1% higher than those in the CK, Si115Mn0, and Si0Mn200 treatments. The highest promoting effect on root biomass was observed at the concentration of 115 mg·kg^{-1} Si and 600 mg·kg^{-1} Mn, which was 90.6%, 52.3%, and 50.2% higher than those in the CK, Si115Mn0, and Si0Mn200 treatments.

Table 2. Two-way ANOVA of the effects of Mn, Si, and Mn×Si interaction treatments on the growth of *C. hystrix* seedling

Factor	**DF**	**Root biomass**		**Stem biomass**		**Leaf biomass**		**Total biomass**	
		***F* value**	***P* value**	***F* value**	***P* value**	***F* value**	***P* value**	***F* value**	***P* value**
Si	3	25.06	$P < 0.001$	27.77	$P < 0.001$	103.45	$P < 0.001$	90.10	$P < 0.001$
Mn	4	39.32	$P < 0.001$	26.16	$P < 0.001$	87.27	$P < 0.001$	90.30	$P < 0.001$
Mn×Si	12	9.54	$P<0.001$	3.65	$P<0.001$	9.30	$P<0.001$	8.71	$P<0.001$

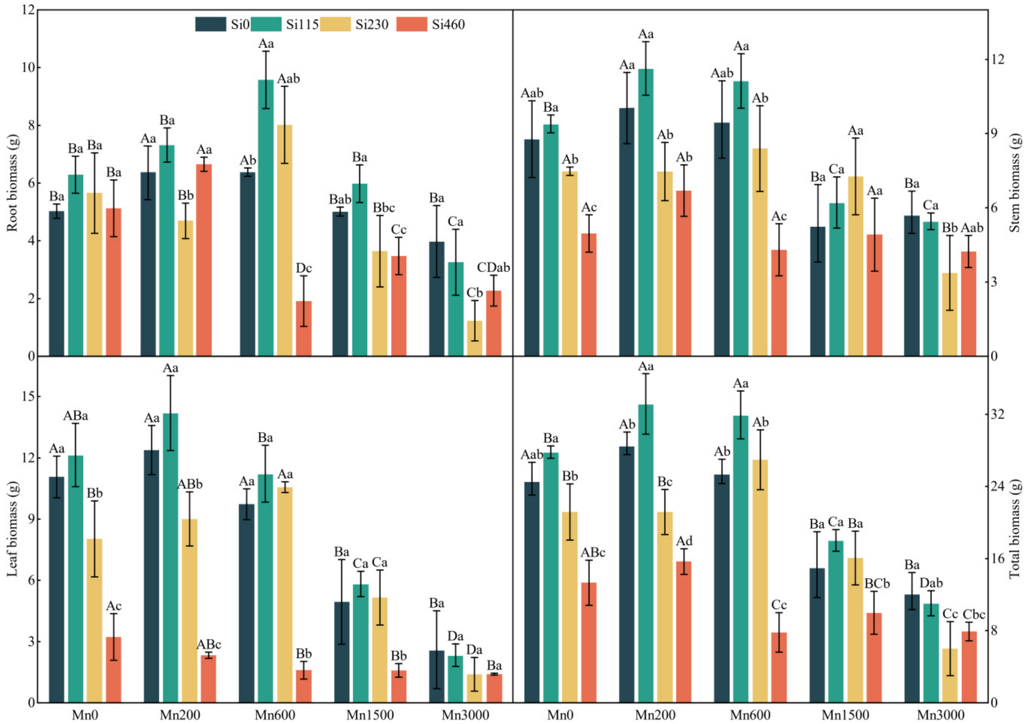

Figure 1. The growth of *C. hystrix* seedling in different Mn and Si treatments

*Notes: Different lowercase letters indicate that the effect is significantly different on different Si treatments in the same Mn treatment, and different capital letters indicate that the effect is significantly different on different Mn treatments in the same Si treatment.

Photosynthetic pigments in different Si and Mn treatments

Results from Table 3 and Figure 2 showed that the Si, Mn, and Si × Mn interaction treatments significantly influenced the photosynthetic pigments (Chl a, Chl b, Chl a+b, Car) of *C. hystrix* seedlings. In the absence of Mn treatment, the contents of photosynthetic pigments decreased with the increasing Si concentration. In the presence of Mn200, the contents of Chl a and Car decreased with the increasing Si concentration, while the contents of Chl b and Chl a+b firstly increased with the addition of 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn600, Mn1500 and Mn3000, the contents of photosynthetic pigments increased with the addition of 115 and 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the absence of Si or in the presence of Si115 and Si230, the contents of photosynthetic pigments significantly decreased with the increasing Si concentration. In the presence of Si460, the contents of Chl a and Chl a+b firstly increased with the addition of 200 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. The content of Car decreased with the increasing Mn concentration.

Table 3. Two-way ANOVA of the effects of Mn, Si, and Mn×Si interaction treatments on photosynthetic pigments of *C. hystrix* seedling

Factor	**DF**	**Chlorophyll a (Chl a)**		**Chlorophyll b (Chl b)**		**Chlorophyll a+b (Chl a+b)**		**Carotenoids (Car)**	
		F value	**P value**	**F value**	**P value**	**F value**	**P value**	**F value**	**P value**
Si	3	269.43	$P < 0.001$	281.19	$P < 0.001$	387.33	$P < 0.001$	103.40	$P < 0.001$
Mn	4	261.14	$P < 0.001$	130.74	$P < 0.001$	299.98	$P < 0.001$	155.02	$P < 0.001$
Mn×Si	12	15.23	$P < 0.001$	14.60	$P < 0.001$	20.58	$P < 0.001$	11.43	$P < 0.001$

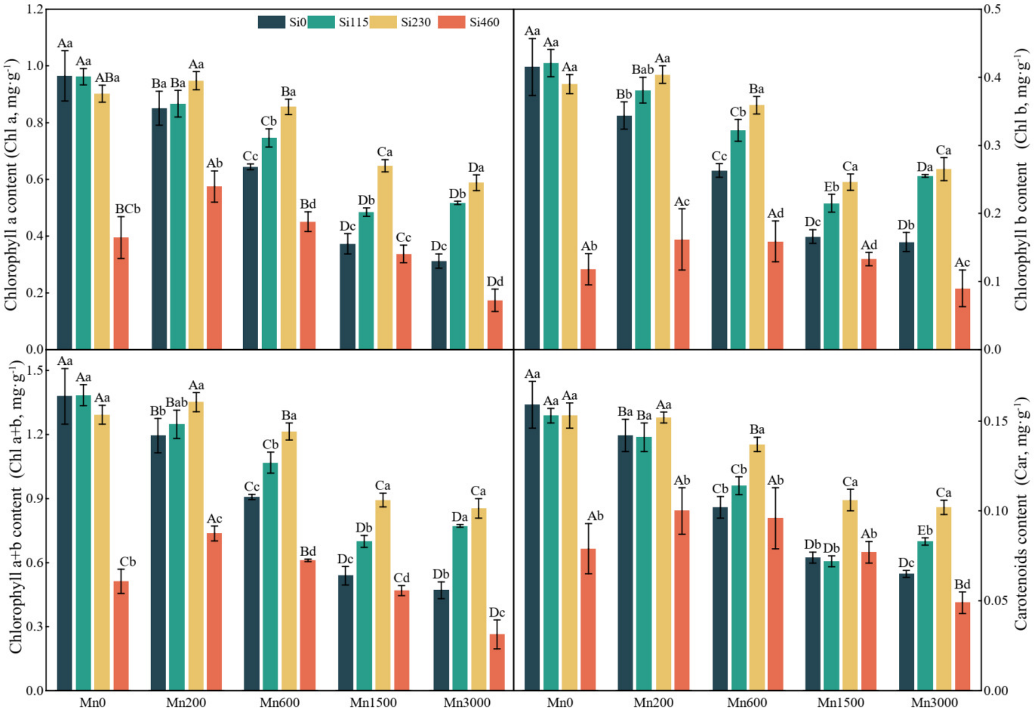

Figure 2. Photosynthetic pigments of *C. hystrix* seedling in different Mn and Si treatments

*Notes: Different lowercase letters indicate that the effect is significantly different on different Si treatments in the same Mn treatment, and different capital letters indicate that the effect is significantly different on different Mn treatments in the same Si treatment.

Photosynthetic indexes in different Si and Mn treatments

Results from Table 4 and Figure 3 showed that the Si, Mn, and Si×Mn treatments significantly influenced the photosynthetic indexes (Gs, Tr, Pn and Ci) of *C. hystrix* seedlings. In the absence of Mn treatment, the Pn, Gs, and Tr firstly increased with the addition of 115 and 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn200, the photosynthetic indexes firstly increased with the addition of 115 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the presence of Mn600 treatment, the photosynthetic indexes decreased with the increasing Si concentration. In the presence of Mn1500 and Mn3000, the Pn, Gs, and Tr firstly increased with the addition of 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration. In the absence or presence of Si treatment, the Pn firstly increased with the addition of 200 or 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. The Ci decreased with the increasing Mn concentration. In the absence of Si or in the presence of Si115 and Si230 treatment, the Gs firstly increased with the addition of 200 or 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. In the absence of Si or in the presence of Si115, the Tr firstly increased in the presence of 200 or 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. In the presence of Si230 and Si460, the Tr decreased with the increasing Mn concentration.

Table 4. Two-way ANOVA of the effects of Mn, Si, and Mn×Si interaction treatments on photosynthetic indexes of *C. hystrix* seedling

Factor	DF	Net photosynthetic rate (Pn)		Stomatal conductance (Gs)		Intercellular carbon dioxide concentration (Ci)		Transpiration rate (Tr)	
		F value	P value	F value	P value	F value	P value	F value	P value
Si	3	83.09	$P < 0.001$	122.30	$P < 0.001$	31.79	$P < 0.001$	31.37	$P < 0.001$
Mn	4	60.37	$P < 0.001$	108.37	$P < 0.001$	36.73	$P < 0.001$	61.16	$P < 0.001$
Mn× Si	12	7.88	$P < 0.001$	18.16	$P < 0.001$	3.40	$P < 0.001$	9.12	$P < 0.001$

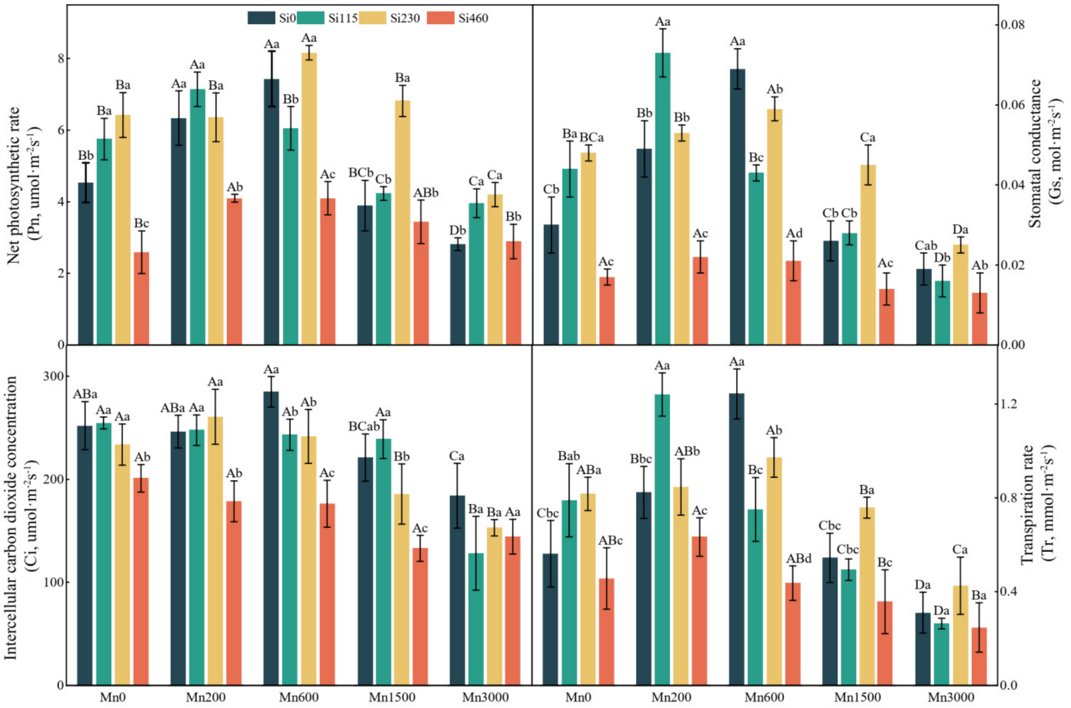

Figure 3. Photosynthesis indexes of *C. hystrix* seedling in different Mn and Si treatments

*Notes: Different lowercase letters indicate that the effect is significantly different on different Si treatments in the same Mn treatment, and different capital letters indicate that the effect is significantly different on different Mn treatments in the same Si treatment.

Chlorophyll fluorescence parameters in different Si and Mn treatments

Results from Table 5 and Figure 4 showed that the Si and Mn treatments significantly influenced the chlorophyll fluorescence parameters of *C. hystrix* seedlings, and the Si×Mn interaction treatments significantly influenced the Fv/Fm, qN, qP and ETR except for the Y(II). In the absence of Mn or in the presence of Mn200 treatment, the Fv/Fm, qN and ETR decreased with the increasing Si concentration. In the presence of Mn600, the Fv/Fm firstly increased with the addition of 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration, but the qN, ETR and qP decreased with the increasing Si concentration. In the presence of Mn1500, the ETR and qP firstly increased with the addition of 230 mg·kg^{-1} Si and then decreased with the increasing Si concentration, while the Fv/Fm and qN decreased with the increasing Si concentration. In the presence of Mn3000, the Fv/Fm firstly increased with the addition of 115 mg·kg^{-1} Si and then decreased with the increasing Si concentration, while the qN and qP decreased with the increasing Si concentration. In the absence or presence of Si treatment, the qP firstly increased with the addition of 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration, while ETR decreased with the increasing Mn concentration. In the presence of Si115 treatment, ETR firstly increased with the addition of 200 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration, while the qP decreased with the increasing Mn concentration. In the presence of Si230 treatment, the Fv/Fm, qP and ETR firstly increased with the addition of 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration. In presence of Si460 treatment, the ETR firstly increased with the addition of 600 mg·kg^{-1} Mn and then decreased with the increasing Mn concentration.

Table 5. Two-way ANOVA of the effects of Mn, Si, and Mn×Si interaction treatments on Chlorophyll fluorescence parameters of *C. hystrix* seedling

Source	DF	Maximum photochemical efficiency of PSII (Fv/Fm)		Efficient quantum yield of PSII Y(II)		Non-photochemical quenching (qN)		Photochemical quenching (qP)		Linear rate of photosynthetic electron transport (ETR)	
		***F* value**	***P* value**	***F* value**	***P* value**	***F* value**	***P* value**	***F* value**	***P* value**	***F* value**	***P* value**
Si	3	37.97	$P <$ 0.001	16.68	$P <$ 0.001	31.53	$P <$ 0.001	14.09	$P <$ 0.001	20.35	$P <$ 0.001
Mn	4	11.76	$P <$ 0.001	6.28	$P <$ 0.001	4.26	$P <$ 0.001	50.79	$P <$ 0.001	53.77	$P <$ 0.001
Mn×Si	12	3.98	$P <$ 0.001	1.74	$P <$ 0.001	2.78	$P <$ 0.001	4.81	$P <$ 0.001	8.05	$P <$ 0.001

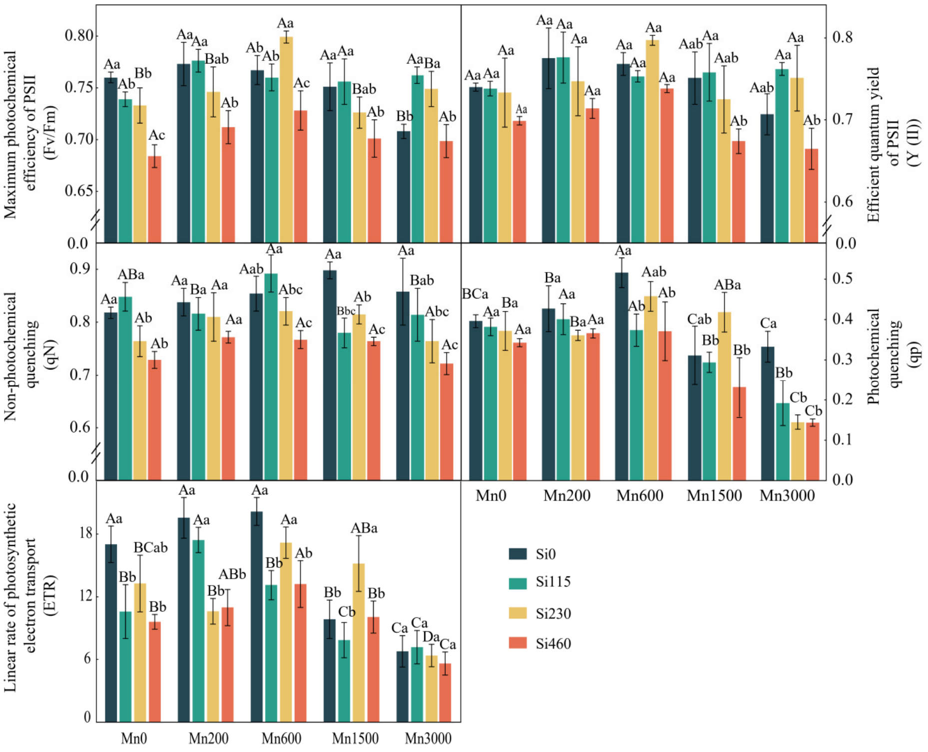

Figure 4. Chlorophyll fluorescence parameters of *C. hystrix* seedling in different Mn and Si treatments

*Notes: Different lowercase letters indicate that the effect is significantly different on different Si treatments in the same Mn treatment, and different capital letters indicate that the effect is significantly different on different Mn treatments in the same Si treatment.

The relationship of plant growth and photosynthesis

Three types of (positive, stagnant, and negative) growth were observed in the clustering analysis, which was basically consistent with the results of the growth of *C. hystrix* seedlings (Figure 5a). In positive growth, the first and second axes explained 73% of co-variance in plant growth, plant biomass in the low concentrations of Si and Mn treatments (Si concentration ≤ 115 mg·kg^{-1}, and Mn concentration ≤ 600 mg·kg^{-1}) was positively relevant with the photosynthetic index and chlorophyll fluorescence but negatively relevant with the photosynthetic pigments, and the qN (21%), Car (18.1%) and Chl a (9.9%) were three main factors that were responsible for the variation of growth-promoting effect (Figure 5b). In stagnant growth, the first and second axes explained 94.1% of co-variance in plant growth, plant biomass in the medium concentrations of Si (Si concentration ≤ 230 mg·kg^{-1}) with low concentration of Mn interaction treatments (Mn ≤ 600 mg·kg^{-1}) exhibited a lower negative correlation with plant photosynthetic pigments but a positive correlation with the photosynthetic index and chlorophyll fluorescence, and the Gs (14.8%), Tr (14.3%) and Fv/Fm (10.6%) were three main factors that were responsible for the growth retardation effect (Figure 5c). In negative growth, the first and second axes explained 84.2% of co-variance in plant growth, plant biomass in the high concentrations of Si or Mn treatments (Si concentration ≥ 460 mg·kg^{-1}, and Mn ≥ 1500 mg·kg^{-1}) exhibited a higher positive relevance with photosynthesis except for the Fv/Fm, and the qP (19.9%), qN (12.1%) and Gs (8.7%) were were three main factors that were responsible for the growth-limiting effect (Figure 5d).

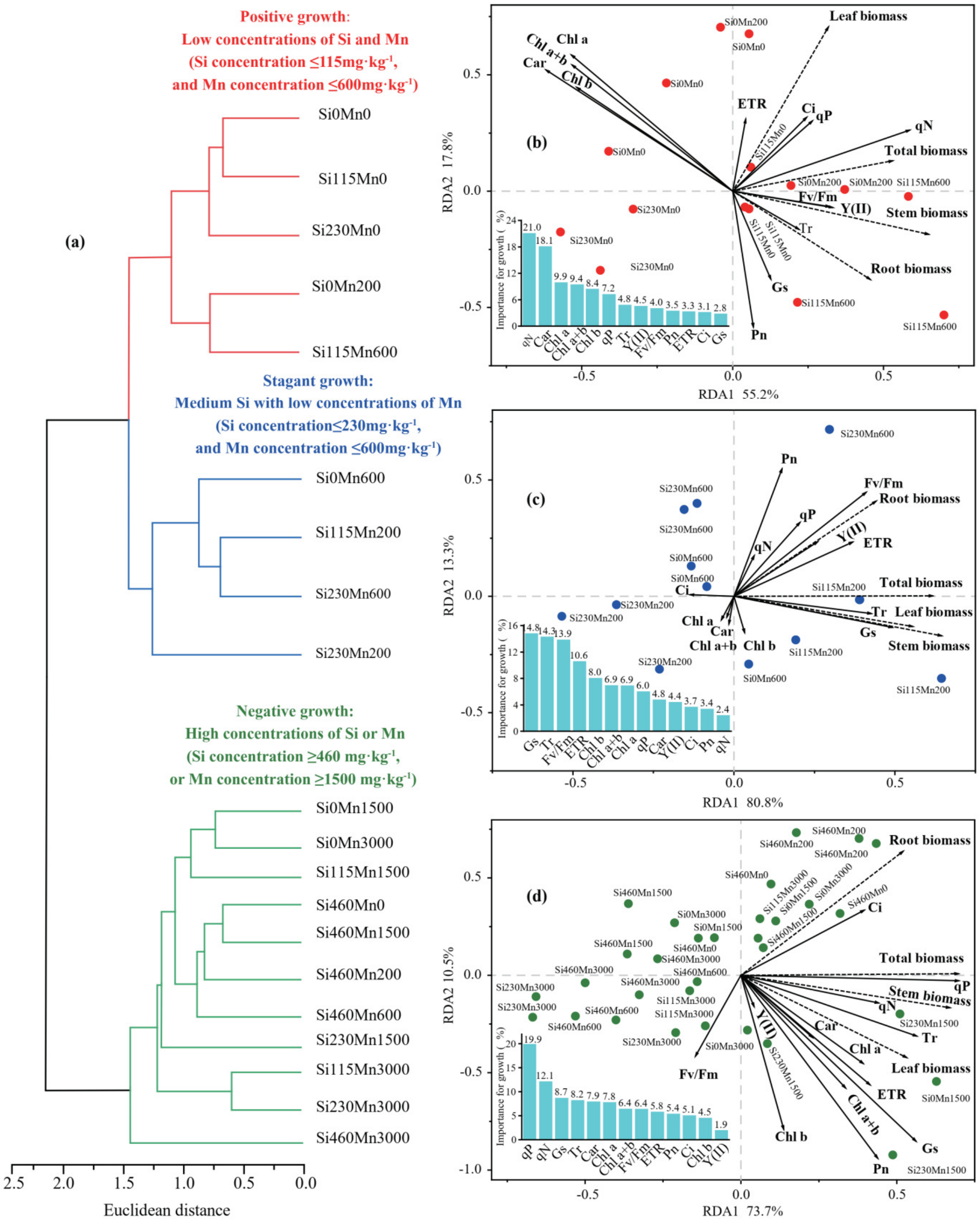

Figure 5. The clustering analysis of *C. hystrix* seedling growth (a), the redundancy analysis and hierarchical partitioning (b-d) between growth and photosynthesis

*Note: The dotted line represents biomass (root, leave, stem, and total biomass), and the solid lines represent the relevant photosynthetic indices (photosynthetic index, chlorophyll fluorescence, and photosynthetic pigments). The abbreviation stands for: Chl a, The content of chlorophyll a; Chl b, the content of chlorophyll b; chlorophyll a+b, the content of; Pn, net photosynthetic rate; Tr, transpiration rate; Ci, intercellular carbon dioxide concentration; Gs, stomatal conductance; Fv/Fm, maximum photochemical efficiency of PSII; Y(II), efficient quantum yield of PSII; qP, photochemical quenching; qN, non-photochemical quenching; ETR, linear rate of photosynthetic electron transport.

Discussion

Effects of Mn and Si treatment on seedling growth and photosynthesis

Photosynthesis is an important process to sense and identify diverse stresses, which is responsible for controlling plant growth, development, and biomass production (Agathokleous *et al.*, 2019; Ghori *et al.*, 2019; Rastogi *et al.*, 2021). In this study, we found that the effect of Si and Mn treatments on plant growth was similar to those photosynthesis indicator (Pn, Gs, Tr, etc). This suggested that the impacts of Si and Mn treatments on plant growth may be related to the changes of photosynthesis indicators. Furthermore, we also found that low doses of Si and Mn could promote the growth of *C. hystrix* seedlings, whereas high doses of Si and Mn could prohibit the growth of *C. hystrix* seedlings. This phenomenon, known as the hormesis effect, were reported by many researchers (Génard *et al.*, 2014; Adrees *et al.*, 2015; Emamverdian *et al.*, 2018; Agathokleous *et al.*, 2019; Rethore *et al.*, 2020). We observed three types of (positive, stagnant, and negative) growth of *C. hystrix* seedlings in different Si and Mn treatments.

Low concentrations of Si and Mn treatments increased plant biomass, and plant biomass was positively correlated with the photosynthetic index and chlorophyll fluorescence but negatively correlated with the photosynthetic pigments. This suggested that low doses of Si or Mn can stimulate the positive growth of *C. hystrix* seedling by regulating stomatal dynamics, photosynthetic pigments and photosynthetic physiology. On the one hand, positive growth of plants can reduce the effects of harmful materials by enhancing the dilution effect (Génard *et al.*, 2014). On the other hand, low doses of Si and Mn act as growth-promoting agent, increasing the light interception capacity, protecting chloroplast functions, and enhancing plant photosynthetic production by increasing the Pn, Gs, and Tr (Arif *et al.*, 2021). Silicon deposition in leaf cells is an active and regulated process that effectively activates the photoprotective mechanism, prevents the overloading excitation energy, and maintains safe heat dissipation by controlling a stable qN and pigments content (de Oliveira Rocha *et al.*, 2022). Manganese also plays an important role in the redox behavior of photosystem II, protecting the processes of photosynthetic physiology (Al-Khayri *et al.*, 2023). As a result, the growth-promoting effect of low concentrations of Si×Mn interaction treatment on *C. hystrix* seedlings was higher than those of low concentrations of Si or Mn treatment. Thus, the application of 115 mg·kg^{-1} Si was an suitable concentration for *C. hystrix* growth under slight Mn-polluted soil.

Medium concentrations of Si ($\leq$ 230 mg·kg^{-1}) with low concentration of Mn interaction treatments showed no effect on the total biomass, indicating that the 230 mg·kg-1 Na_2SiO_3 treatment can cause salt stress in plants, leading to stagnant growth in *C. hystrix* seedlings. To resist salt stress, seedlings actively sacrificed their aboveground biomass production and adopted a subtle growth-survival trade-off to balance the photosynthesis production and stress consumption. This was confirmed by an increase in Pn, Gs, and Tr but a decrease in Ci. Most studies have reported same point that plants actively repress growth under stress conditions as an adaptive strategy to maximize survival (Zhang *et al.*, 2020; Alejandro *et al.*, 2020). The negative correlation between biomass production and photosynthetic pigments indicated that the synthesis of pigments has been limited. But a coordinated allocation of Si and Mn for photosynthetic response and defense pathways can strengthen the chloroplast structure and maximize survival ability (Zeroual *et al.*, 2020; Matanzas *et al.*, 2021). With the aid of Mn and Si, *Castanopsis hystrix* seedlings can still operate a normal photosynthetic response by increasing Fv/Fm. The increase in root biomass equalled to the consumption of the above-ground, which also reflected that *C. hystrix* seedlings maintained a subtle balance between growth and defense. Because root is the first line of defense for plants against stress, while the leaves is the sensitive organ to indicate stress signals (Arif *et al.*, 2021). However, the defense system here needs to be further investigated.

High concentrations of Si or Mn treatments decreased plant biomass, and plant biomass was positively correlated with photosynthesis indicators. This negative growth demonstrated that the photosynthetic growth of *C. hystrix* seedlings was heavily affected by high doses of Si or Mn treatment, and the growth-survival tradeoff was broken and could not reset the balance. One reason for this is that excessive Mn the accumulation in plants caused Mn toxicity, leading to decreased the qP and qN, hindered photosynthetic electron transport, disrupted chloroplast structure, impaired chlorophyll biosynthesis and photosynthetic production (Liang and Teng, 2021; Shi *et al.*, 2023). Additionally, the decline of Gs impaired CO_2 entry into leaves, resulting in decreased photosynthetic rates (Alvarez-Mateos *et al.*, 2019). Another reason is that excessive sodium in plants can cause salt stress, resulting in cytotoxicity and nutritional imbalance (Ponce *et al.*, 2021; Tian *et al.*, 2023). Thus, high doses of Si and Mn interaction treatment may heavily damage the defense system of *C. hystrix* seedlings, resulting in a poor survival capacity, a declined resistance response and a loss of biomass. This also explains why the growth-limiting effect on *C. hystrix* seedlings was lower in high concentrations of Si×Mn interaction treatment compared to high concentrations of Si or Mn treatment.

The silicon-mediated alleviation of Mn toxicity on seedlings

External additives have been found to alleviate various stresses, such as salinity, heavy metal, flooding, heat, and cold (Génard *et al.*, 2014; Emamverdian *et al.*, 2018; Arif *et al.*, 2021). In Si and Mn interaction treatments, our study demonstrated that the addition of Si can act as an alleviating agent in reducing Mn-induced stress. The alleviating effect of low doses of Si under Mn stress is mainly manifested in the following aspects. Firstly, most of the Si absorbed by plants can be deposited in the cell apoplast, playing a supportive role in enhancing cell membrane permeability and resistance, and protecting chloroplast structure and photosynthetic capacity, thus reducing the uptake of Mn (El-Fouly *et al.*, 2011; Fischer *et al.*, 2015). Secondly, previous studies have indicated that Mn stress can induce the generation of reactive oxygen species (ROS), while low dose of Si can effectively scavenge these ROS, safeguarding chloroplast structure and maintaining the ROS homeostasis in production and elimination (Al-Khayri *et al.*, 2023). Thirdly, the addition of Si can improve the absorption and assimilation of micro-nutrients (N, P, K, Ca, Mg, Zn) by increasing root volume, surface area and biomass (Arif *et al.*, 2021). Additionally, leaf falling helps remove the toxic metabolite materials (e.g. Mn, ROS) from the plant (Chen *et al.*, 2023; Tian *et al.*, 2023). We also found that the low dose of Mn can alleviate the growth limitation caused by salt stress. For example, the total biomass in the Si230Mn600 treatment was significantly higher 27.5% in the Si230Mn0 treatment. This is because the addition of Mn effectively improves the absorption of essential elements (Mn, Fe, Zn, Cu), increases the antioxidant enzyme activities in plants, and maintains a normal growth for plants (Lu *et al.*, 2020).

Our results demonstrated that the most suitable concentration of Si was 115 $mg \cdot kg^{-1}$ Si for *C. hystrix's* growth under low Mn stress. However, the underlying mechanisms here are difficult to study due to the complicated physiological response for growth and defense, unclear mechanisms of growth-survival tradeoff, and the complicated interaction network of Si and Mn in plants involving multiple metabolic, physiological and structural adaptation processes (Gul *et al.*, 2022; Jing *et al.*, 2023). Therefore, future experiments are needed to identify the underling mechanisms, including defensive, metabolic, physiological and regulatory networks.

Conclusions

In conclusion, our study demonstrates that the addition of Si and Mn actives the hormesis effects of *C. hystrix* seedlings, influencing biomass, photosynthetic pigments, photosynthetic index, and chlorophyll fluorescence. Three types of (positive, stagnant, and negative) growth of *C. hystrix* seedlings were observed in response to different Si and Mn treatments. Low concentrations of Si and Mn treatments (Si concentration ≤ 115 $mg \cdot kg^{-1}$, and Mn ≤ 600 $mg \cdot kg^{-1}$) can stimulate positive growth of *C. hystrix* seedlings by increasing the Pn, Gs, and Tr. Medium concentrations of Si (≤230 $mg \cdot kg^{-1}$) with low concentration of Mn treatments can lead to stagnant growth of *C. hystrix* seedlings by increasing Gs, Tr and Fv/Fm but decreasing Ci. High concentrations of Si or Mn treatments can cause negative growth of *C. hystrix* seedlings by decreasing qP, qN, Gs, Pn and pigment contents. Furthermore, the addition of Si could alleviate the stress induced by Mn and drive *C. hystrix* seedlings develop a growth and survival regulatory to avoid stress. Hence, we concluded that the most suitable concentration of Si was 115 mg·kg^{-1} Si for *C. hystrix*'s growth under low Mn stress. Future studies will pay attention to the systematic and in-depth research of the underling mechanisms of defensive, metabolic, physiological and regulatory networks on *C. hystrix* seedlings. This will deepen our research on the adaptation mechanism of *C. hystrix* seedlings and provide a theoretical reference for the cultivation and management of *C. hystrix* artificial forests in Mn-polluted soils.

Authors' Contributions

Conceptualization, formal analysis, visualization, methodology: L.H. and Z.T.; Investigation, resources: L.H., K.L., and W.S.; Writing–original draft preparation, L.H. and Z.T.; Writing, review and editing: Z.T., K.L., W.T. and W.S.; All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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