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Physiological and Biochemical Adaptation of Common Garden Plants to Inorganic Nitrogen-Laden Fine Particulate Matter Stress

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Abstract: Accelerated urbanization has intensified nitrogen deposition and fine particulate matter ($PM_{2.5}$) pollution. While urban landscape plants play a vital role in atmospheric remediation, systematic exploration of their adaptation strategies to these dual stressors remains limited. This study investigated the dynamic responses of antioxidant defense systems and nitrogen/weight ratios of *Iris germanica* L. and *Portulaca grandiflora* Hook. under four nitrogen deposition scenarios (N0, N1, N2, and N4 with nitrogen concentrations of 0, 15, 30, and 60 kg $N \cdot hm^{-2} \cdot a^{-1}$, respectively) combined with constant $PM_{2.5}$ exposure (50 $\mu g/m^3$). Through fumigation experiments, we demonstrated that *Iris germanica* L. showed higher sensitivity to inorganic nitrogen-laden $PM_{2.5}$ stress than *Portulaca grandiflora* Hook. Both species exhibited stronger antioxidant enzyme (SOD, CAT, POD) activities in the high-growth season compared to the low-growth season. Nitrogen allocation analysis revealed that *Portulaca grandiflora* Hook. maintained stable nitrogen content across treatments, while *Iris germanica* L. showed progressive nitrogen loss under high nitrogen-laden $PM_{2.5}$ exposure. These findings establish *Portulaca grandiflora* Hook.'s superior resilience through two synergistic mechanisms: modulated antioxidant systems and efficient nitrogen remobilization. This comparative study provides actionable insights for selecting pollution-tolerant species in urban green infrastructure planning.

Keywords: urban air pollution; $PM_{2.5}$ exposure; nitrogen metabolism; antioxidant defense; plant stress tolerance; urban landscaping

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Academic Editor: Bartolomeo Dichio

Received: 12 February 2025
Revised: 7 March 2025
Accepted: 17 March 2025
Published: 20 March 2025

Citation: Xiao, K.; Wang, Y.; Wang, R.; Hu, Z.; Peng, S.; Miao, Z.; Ge, Z. Physiological and Biochemical Adaptation of Common Garden Plants to Inorganic Nitrogen-Laden Fine Particulate Matter Stress. *Horticulturae* **2025**, *11*, 337. https://doi.org/10.3390/horticulturae11030337

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1. Introduction

The concurrent escalation of atmospheric nitrogen deposition and particulate matter (PM) pollution has emerged as a critical environmental stressor driven by global urbanization and industrialization [1,2]. These interconnected phenomena profoundly affect both ecosystem integrity and public health through multiple pathways [3–5]. Atmospheric reactive nitrogen (Nr) concentrations exhibit a sustained upward trajectory [6], with excess Nr undergoing heterogeneous chemical transformations that generate nitrogenous compounds adsorbed onto PM surfaces, thereby exacerbating aerosol pollution through secondary formation processes [7].

As an essential macronutrient, nitrogen governs fundamental metabolic pathways in plant systems [8]. While nitrogen has been demonstrated to enhance plant growth and

productivity within optimal concentration ranges [9], supra-optimal nitrogen accumulation in plant tissues can exert growth-inhibitory effects upon reaching nitrogen saturation thresholds [10]. Nitrogen deposition-induced excess may adversely affect plant physiology, morphology, and stress tolerance. At the physiological level, excessive nitrogen disrupts nitrogen metabolism, alters nutrient homeostasis, and impairs photosynthetic efficiency, resulting in reduced net photosynthetic rates [11]. In terms of morphology, nitrogen overaccumulation induces foliar abscission and chlorosis [12] while simultaneously compromising plant resilience to environmental stressors, including drought [13], low-temperature conditions, and pest infestation. Notably, plant responses to nitrogen deposition exhibit species-specific variations dependent not only on ambient nitrogen ratios but also on functional group classifications. Of particular significance, divergent nitrogen use efficiencies occur between photosynthetic types, with C4 plants displaying significantly higher nitrogen utilization capacity than C3 species [14]. Correspondingly, nitrogen supplementation exerts more pronounced effects on biomass accumulation and growth rates in C3 plants relative to C4 counterparts [15].

Airborne PM, a critical component of airborne pollutants, is classified as TSP (Total Suspended Particulate, Dp $\leq$ 100 μm), PM10 (Dp $\leq$ 10 μm), $PM_{2.5}$ (Dp $\leq$ 2.5 μm), etc., according to the aerodynamic diameter of the PM. PM less than 2.5 μm is also known as fine PM. Chemical characterization reveals that water-soluble inorganic ions dominate $PM_{2.5}$ composition, contributing approximately 50% of its mass fraction [16], with ammonium (NH_4^+) and nitrate (NO_3^-) emerging as the predominant ionic species [17].

Plants function as a natural filtration system through foliar PM interception, with plants demonstrating significant capacity for particulate matter absorption and retention. This biological process establishes plants as an essential component in urban PM pollution mitigation strategies [18,19]. However, PM accumulation on phyllosphere surfaces induces detrimental physiological impacts. Mechanistic studies demonstrate dual pathway interference with photosynthesis: (1) surface-deposited particulates attenuate photosynthetically active radiation penetration, and (2) stomatal occlusion by particulate deposits impedes gaseous exchange processes [20]. These synergistic effects depress key photosynthetic parameters, including net photosynthetic rate and stomatal conductance, while simultaneously initiating oxidative stress through reactive oxygen species (ROS) generation, consequently elevating antioxidant enzyme activities [21,22]. However, plant response to PM is highly dependent on particle concentrations and species-specific tolerance thresholds. Comparative studies reveal divergent physiological responses under equivalent $PM_{2.5}$ exposure: *Koelreuteria paniculata* demonstrates a 50% enhancement in antioxidant enzyme activity at 200 μg/m^3, while Trifolium repens sustains irreversible oxidative damage under identical conditions [23]. Tolerance mechanisms show marked differentiation: *Platycladus orientalis* (Chinese arborvitae) showed enhanced ROS scavenging capacity at $PM_{2.5}$ levels > 150 μg/m^3, with ascorbic acid (AsA) content increasing by 50% and superoxide dismutase (SOD) activity increasing by 35%. Conversely, sensitive species such as *Toxicodendron vernicifluum* (Japanese lacquer tree) showed only a 15% increase in AsA, resulting in an air pollution tolerance index (APTI) below 8.0—a threshold indicating low resilience to pollution [24]. Beyond these biochemical strategies, morphological traits critically determine interspecific PM retention efficiency. Evergreen shrubs in Beijing, including *Cephalotaxus sinensis* and *Euonymus japonicus*, achieved superior $PM_{2.5}$ trapping efficiencies (1.5–2.0 μg/cm^2) due to rough leaf surfaces and dense trichomes, which enhance particle adhesion [25]. This biomechanical optimization parallels Tectona grandis (teak) specimens in Indian coalfields, which demonstrate exceptional PM resilience (APTI = 17.0) attributed to thick cuticular wax layers that prevent stomatal blockage while maintaining gas exchange efficiency [26].

At present, scholars have made some progress in studying the effects of nitrogen deposition and PM on plants, but most of them have focused on natural ecosystems such as forests and farmlands, and relatively few studies have been conducted on urban landscape plants, and most of these have focused on growth performance or changes in a single physiological index. In addition, due to the complexity and variability of urban environments, the responses of different types of landscape plants to nitrogen-laden PM may differ significantly, further increasing the complexity and challenge of the study.

Iris germanica L. and *Portulaca grandiflora* Hook. are herbaceous plants renowned for their ornamental and medicinal properties [27–29]. They possess remarkable environmental adaptability, which has made them popular choices for urban greening and landscaping. In particular, they are widely used as ground cover in urban green spaces in southern China. Although previous research on their stress resistance has mainly focused on drought and salinity tolerance [30–32], the adaptive mechanisms of these two species under nitrogen deposition and atmospheric particulate pollution remain poorly understood.

In this study, we investigated the physiological and biochemical adaptation of *Iris germanica* L. and *Portulaca grandiflora* Hook. to inorganic nitrogen-laden fine particulate matter (hereafter abbreviated as nitrogen-laden $PM_{2.5}$) stress. The main objectives of this study were as follows: (1) to bring new contributions to the regulatory mechanisms of plant nitrogen storage patterns and antioxidant defense systems under varying levels of particulate pollution and (2) to compare the physiological responses of these two representative garden species under identical pollution conditions and explore the reasons and potential mechanisms for the differences in their tolerance. The results of this study are expected to provide a theoretical basis for optimizing plant selection and allocation in urban landscaping against the background of increasing nitrogenous $PM_{2.5}$ in air pollution. It is also expected to improve our understanding of the response mechanisms by which plants respond to nitrogenous $PM_{2.5}$ pollution.

2. Materials and Methods

2.1. Study Area

This experiment was carried out at the Jishan Experimental Forestry Farm of the Jiangsu Academy of Forestry in Jiangning District, Nanjing, China (31°32°07′ N, 118°119°06′ E). The experimental site is situated in the north subtropical monsoon climate zone, characterized by an annual average temperature of 15.7 °C and abundant rainfall with an annual average precipitation of 1072.9 mm. The study region experiences extreme temperature fluctuations, with an annual minimum of −13.3 °C and a maximum of 40.4 °C during severe weather events. Between 2009 and 2011, the wet and dry deposition of inorganic nitrogen in Nanjing was 28.7 kg $N{\cdot}hm^{-2}{\cdot}a^{-1}$ and 35.8 kg $N{\cdot}hm^{-2}{\cdot}a^{-1}$, respectively [33]. From 2014 to 2016, the average yearly concentrations of $PM_{2.5}$ in Nanjing ranged from 43 to 74 μg m^{-3} [34].

2.2. Experimental Design

The experiment was conducted in an unheated greenhouse at the Jiangsu Academy of Forestry (Nanjing, China), where temperature and humidity conditions mirrored the indoor environment. The natural temperature range was 18–28 °C, and the average relative humidity was 65 ± 10%, which is consistent with local indoor values. Photosynthetically active radiation (PAR) was maintained at 250–400 μmol/m^2/s during the day by natural sunlight filtered by polycarbonate panels. *Iris germanica* L. and *Portulaca grandiflora* Hook. were sown in February in cylindrical plastic pots (top diameter: 15 cm; bottom diameter: 13 cm; height: 15 cm; approximate volume: 1.7 L) filled with a uniform nursery substrate (Model 422, Klasmann-Deilmann GMBH Incorporated, Geeste, Germany).

Separate fumigation experiments were conducted for the *Iris germanica* L. and *Portulaca grandiflora* Hook., with each plant exposed to four distinct fumigation concentration treatments and aerosol levels as follows: N0 (aerosol with an average particle size of 2.5 μm from distilled water, nitrogen concentration = 0 kg $N \cdot hm^{-2} \cdot a^{-1}$), N1 (aerosol formed from NH_4NO_3 solution with an average particle size of 2.5 μm, nitrogen concentration = 15 kg $N \cdot hm^{-2} \cdot a^{-1}$), N2 (same as above, nitrogen concentration = 30 kg $N \cdot hm^{-2} \cdot a^{-1}$), and N4 (same as above, nitrogen concentration = 60 kg $N \cdot hm^{-2} \cdot a^{-1}$). The nitrogen concentrations were determined according to the annual nitrogen deposition levels in Nanjing City. For each fumigation concentration, four individual plants with virtually identical growth patterns were selected as subjects for both *Iris germanica* L. and *Portulaca grandiflora* Hook., resulting in a total of 32 plants.

2.3. Test Equipment

Utilizing a custom-designed fumigation system (Figure 1) with proprietary intellectual property rights (Patent No: ZL201621111648.7, China) [35], the experimental setup comprises three primary components: a $PM_{2.5}$ generator, plant chambers, and an exhaust gas recycling device. The $PM_{2.5}$ generator is composed of an air pump (Model 36-7, Jiebao Incorporated, Shanghai, China) and a six-nozzle aerosol generator (Model: 9306A, TSI Incorporated, Shoreview, MN, USA), which produces NH_4NO_3 aerosols with a median particle size of 2.5 μm. The particle size is calibrated through the nozzle of the regulator and monitored using a Dusttrak II particulate monitor (Model: 8530, TSI Incorporated, Shoreview, MN, USA), which was only turned on for concentration checking during fumigating. The plant chambers, constructed from Plexiglas, feature a rectangular design measuring 0.3 m × 0.3 m × 0.65 m with a side sliding door. To prevent the absorption of aerosol particles from being absorbed by the soil, a plastic film covers the soil surface. For irrigation purposes, an irrigation tube is inserted into the soil using a PVC pipe and securely capped. The entire apparatus was sealed to facilitate gas circulation, with exhaust gases directed through the exhaust pipe into an exhaust gas collection pool containing $NaHCO_3$ solution to mitigate environmental contamination. Fans were installed both vertically and horizontally in each chamber for the uniform distribution of aerosols, temperature, and CO_2.

The experiment operated for 16 h each daily, with a scheduled 1 h break for every 2 h of operation to maintain a consistent $PM_{2.5}$ concentration within the system at 50 μg m^{-3} (in accordance with the annual average $PM_{2.5}$ concentration in Nanjing).

2.4. Sample Collection and Sample Analysis

Sampling was carried out on the 3rd, 8th, 15th, 22nd, and 30th days starting from 1 April (considered the low-growth season of the plants) and 15 July 2018 (the high-growth season of the plants). Subsequently, two leaves exhibiting uniform length, complete shape, good health, and consistent maturity were carefully selected from each potted plant. These carefully selected leaves were then carefully removed and stored in an icebox for transportation to the laboratory for the determination of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities of the plants. Furthermore, a portion of leaves and roots were harvested from each potted plant for subsequent drying and grinding into a fine powder, passing through a 0.149 mm steel sieve, and then utilized for the assessment of the plants' total nitrogen/weight ratio using a PE2400II Elemental Analyser (PEKIN-ELMER Co., Ltd., Waltham, MA, USA).

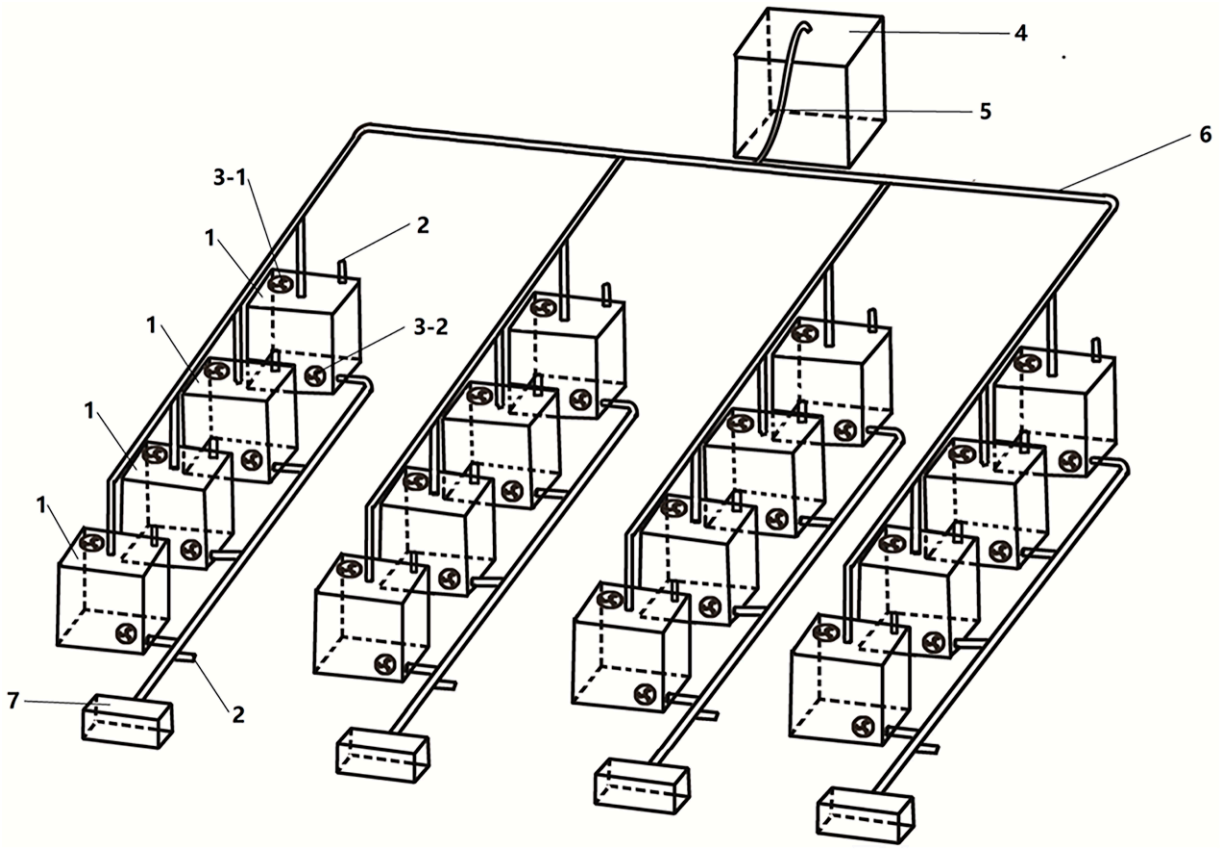


Figure 1. Schematic diagram of the device structure of the experimental device (Patent No: ZL201621111648.7, China) [35]. Note: 1 represents test plant chamber, 2 represents concentration-monitoring port, 3-1 represents vertical fan, 3-2 represents horizontal fan, 4 represents aerosol generator, 5 represents rubber hose, 6 represents PVC tube, and 7 represents alkaline absorber.

Approximately 0.2 g of fresh leaves were accurately weighed and incised, following which 10 mL of pre-cooled PBS 7.8 solution was sequentially added in two installments. The samples were ground and extracted, followed by centrifugation at 10,500 rpm for 15 min at 4 °C [35]. The resulting supernatant was collected for subsequent enzyme assays and stored at 4 °C. For the assessment of SOD activity measurement, the nitro blue tetrazolium photoreduction method, as described by Giannopolitis and Ries [36], was employed, with 50% inhibition of nitro blue tetrazolium (NBT) photochemical reduction considered as one unit of enzyme activity. POD activity was determined through guaiacol oxidation following the method outlined by Zheng and Van Huystee [37], with an increase of 0.01 per minute in optical density (OD) at 470 nm, defined as one unit of activity. Lastly, CAT activity was evaluated via UV absorption following the method established by Change and Maehly [38], with a decrease of 0.01 per minute in OD at 240 nm considered as one unit of enzyme activity.

2.5. Statistical Analyses

The preliminary data processing was carried out using Excel 2016, followed by the utilization of SPSS 25.0 software (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. IBM Corp.: Armonk, NY, USA) for performing multifactorial ANOVA on plant antioxidant enzyme activity based on growth period, fumigation time, fumigation concentration, and plant species. Moreover, one-way ANOVA was performed on antioxidant enzyme activity considering fumigation time, nitrogen pattern, and fumigation concentration, while repeated measures ANOVA was employed to analyze antioxidant enzyme activity with respect to fumigation concentration. Prior to the repeated measures ANOVA,

Mauchly's sphericity test [39] was conducted, and the significance of the differences between factors was reported post Mauchly's sphericity test confirmation. In instances where Mauchly's sphericity test did not meet the assumptions, the Greenhouse–Geisser was applied. The statistically significance level was established at $p < 0.05$. Graphical representations were generated utilizing Origin 2021 software (version 2021 for Windows; OriginLab. MAS, Hampton, VA, USA).

3. Results

3.1. Effects of Inorganic Nitrogen-Laden Fine PM on Antioxidant Systems in Iris germanica L. and Portulaca grandiflora Hook.

ANOVA analysis revealed that all four factors of the growth period, fumigation time, fumigation concentration, and plant species significantly influenced the changes in the activities of the three enzymes, while the exception of plant species did not exhibit a significant effect on the changes in POD activities (Table 1). Overall, the analysis highlights complex interdependencies among factors, the combined effects of these factors play important roles in modulating the activity of antioxidant enzyme activities.

Table 1. ANOVA analysis for the effects of growth stage, plant species, fumigation concentration, fumigation time, and their interactions on plant antioxidant enzyme activities.

Indexes	SOD		POD		CAT	
	F	**P**	**F**	**P**	**F**	**P**
Stage (S)	13.496	***	389.110	***	101.999	***
Plant (P)	9.675	**	0.343	NS	3545.908	***
Concentration (C)	115.293	***	15.283	***	26.914	***
Time (T)	104.232	***	185.639	***	442.188	***
S × P	161.042	***	221.821	***	1.303	NS
S × C	7.706	***	0.961	NS	16.166	***
S × T	41.691	***	151.212	***	78.761	***
P × C	12.998	***	21.516	***	45.363	***
P × T	42.304	***	59.682	***	54.925	***
C × T	5.098	***	5.749	***	19.204	***
S × P × C	0.695	NS	15.087	***	31.297	***
S × P × T	23.368	***	23.783	***	14.019	***
S × C × T	4.969	***	5.499	***	15.425	***
P × C × T	4.846	***	10.407	***	32.018	***
S × P × C × T	2.351	**	6.046	***	33.128	***

Abbreviations: SOD, POD, CAT for superoxide dismutase, peroxidase, and catalase, respectively. Bold characters indicate significant differences. **, and *** p values are less than 0.01, and 0.001, respectively. NS is not statistically significant.

3.1.1. Effect of Fumigation Time on Antioxidant Enzyme Activity

The comparison of trends in antioxidant enzyme activities within the same plant across varying fumigation times in different growth periods revealed distinct patterns. A notable observation was the earlier increase in SOD activity for both *Iris germanica* L. and *Portulaca grandiflora* Hook. during the high-growth season compared with that in the low-growth season, indicating a more rapid and consistent response to stress in both species during active growth (Figure 2). Moreover, there was no significant downward trend observed in POD activities for both *Iris germanica* L. and *Portulaca grandiflora* Hook. towards the latter phase of the fumigation period in the high-growth season (Figure 3). This suggests the plants' improved capacity to sustain POD activity under stress conditions during the growing phase. The fluctuations in CAT activity of *Iris germanica* L. and *Portulaca grandiflora* Hook. were more pronounced during the late fumigation period of the low-

growth season while exhibiting a more moderate variation during the fumigation period of the high-growth season (Figure 4). These findings emphasize the plants' capacity to regulate antioxidant enzymes more consistently during active growth phases, indicating a more stable and resilient response to stress.

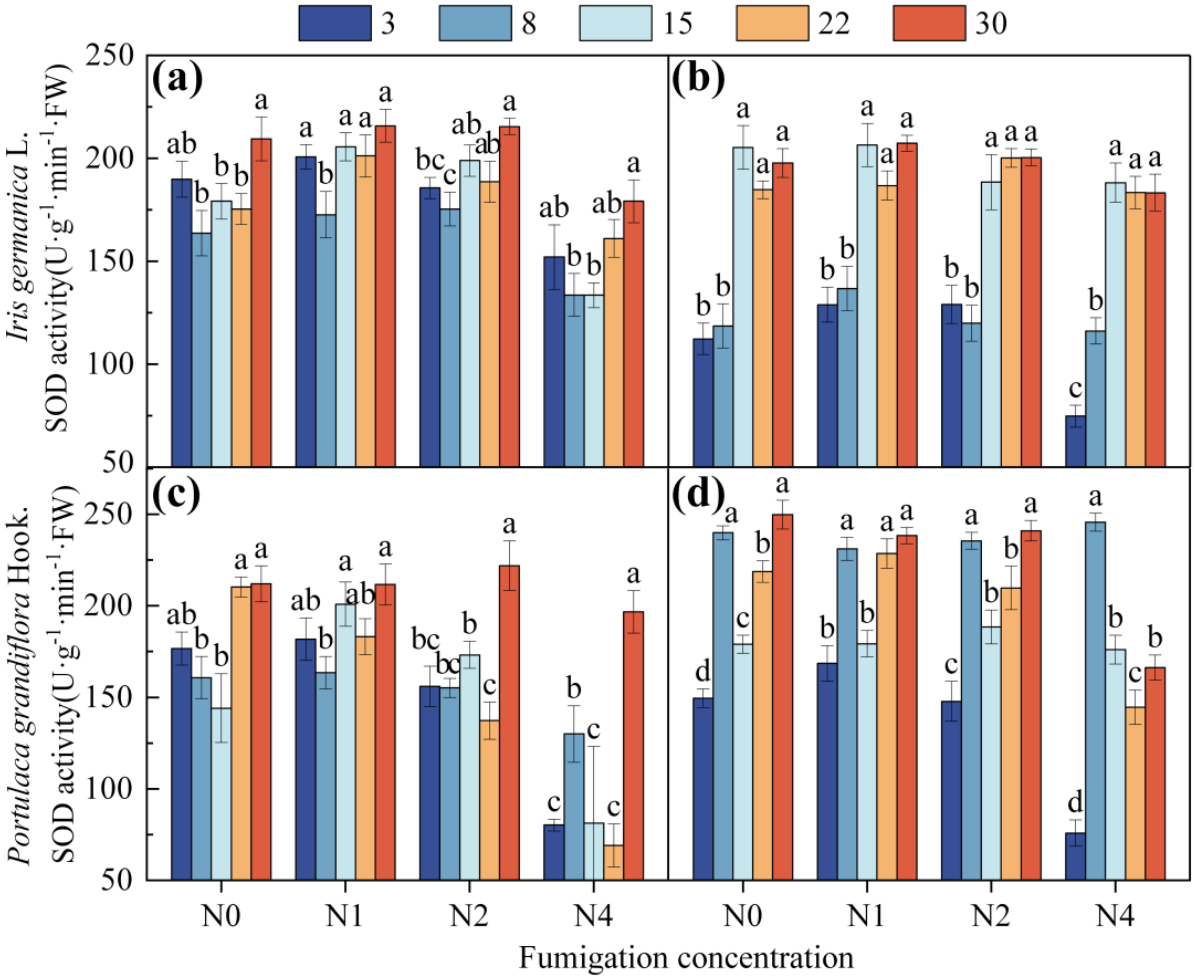


Figure 2. Effect of fumigation time on superoxide dismutase (SOD) of *Iris germanica* L. and *Portulaca grandiflora* Hook. with different growth stages (n = 8). The error bars are standard errors. (**a**,**c**) represent April (low-growth season), and (**b**,**d**) represent July (high-growth season). Different lowercase letters indicate the significant ($p < 0.05$) difference in SOD activity of plants at the same fumigation concentration and at different fumigation times.

Furthermore, it is worth noting that CAT activity exhibited relatively higher levels within the antioxidant enzyme system of *Iris germanica* L., whereas POD activity was significantly elevated in *Portulaca grandiflora* Hook. These distinct enzyme profiles indicate that both CAT and POD play critical roles in scavenging hydrogen peroxide (H_2O_2) ROS, with *Iris germanica* L. primarily depending on CAT for H_2O_2 scavenging and *Portulaca grandiflora* Hook., predominantly utilizing POD for H_2O_2 detoxification.

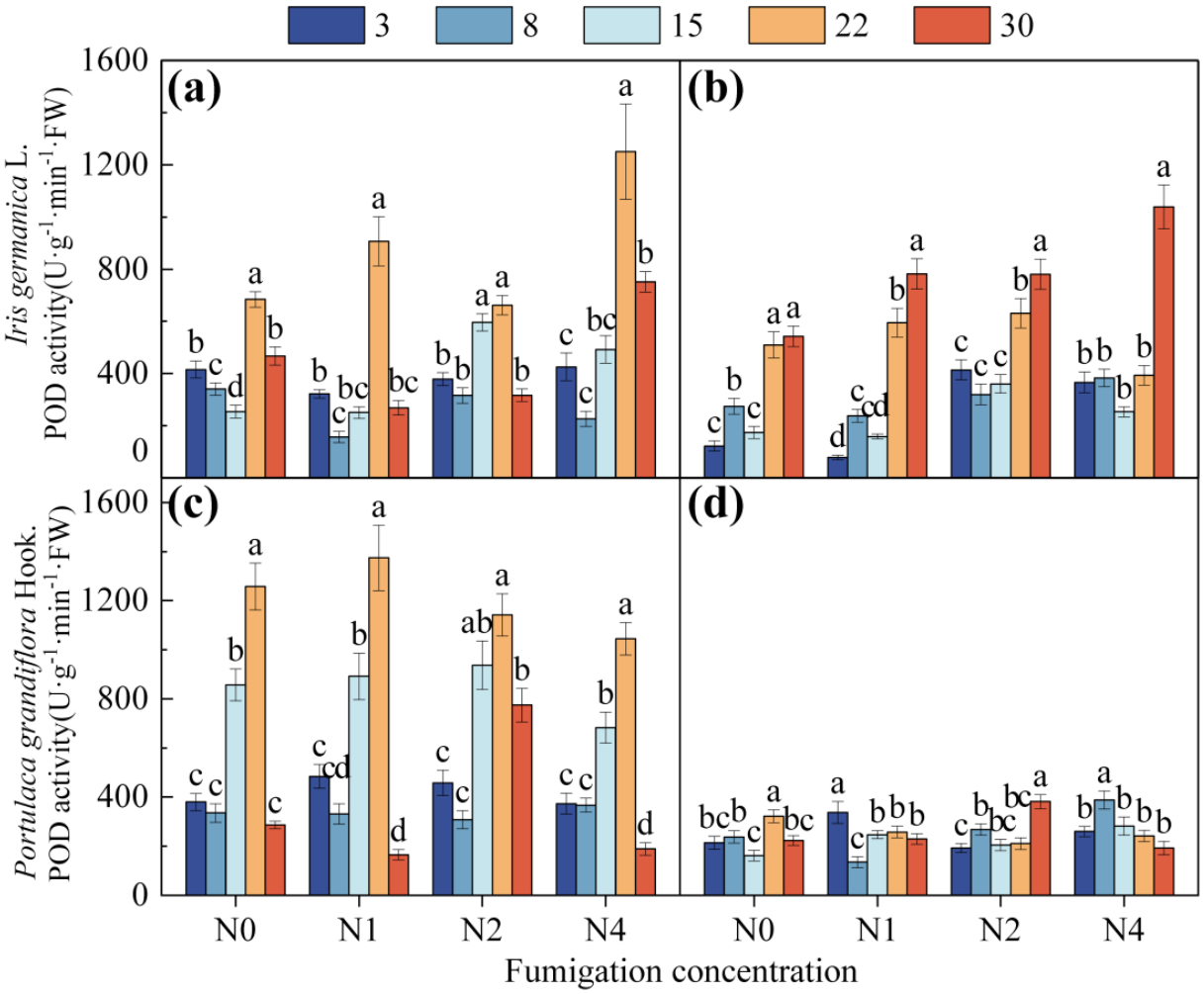


Figure 3. Effect of fumigation time on peroxidase (POD) of *Iris germanica* L. and *Portulaca grandiflora* Hook. with different growth stages (n = 8). The error bars are standard errors. (**a**,**c**) represent April (low-growth season), and (**b**,**d**) represent July (high-growth season). Different lowercase letters indicate the significant ($p < 0.05$) difference in POD activity of plants at the same fumigation concentration and at different fumigation times.

3.1.2. Effect of Fumigation Concentration on Antioxidant Enzyme Activity

Both in the non-growing and high-growth season, the SOD activity of *Iris germanica* L. and *Portulaca grandiflora* Hook. exhibited a significant decrease in the N4 treatment compared with that in the other treatments (Figure 5A,B). In the low-growth season, *Iris germanica* L. POD activity displayed significantly higher in the N4 treatment than the other treatments, while in the high-growth season, both the N2 and N4 treatments were significantly higher than the N0 and N1 treatments. Conversely, *Portulaca grandiflora* Hook. did not demonstrate significant differences in POD activity among other treatments (Figure 5C,D). Furthermore, in the low-growth season, *Iris germanica* L. CAT activity was significantly elevated in the N1 treatment compared with that in the other treatments, with no significant differences observed in the high-growth season. In contrast, *Portulaca grandiflora* Hook. did not exhibit significant variations in CAT activity across treatments (Figure 5E,F).

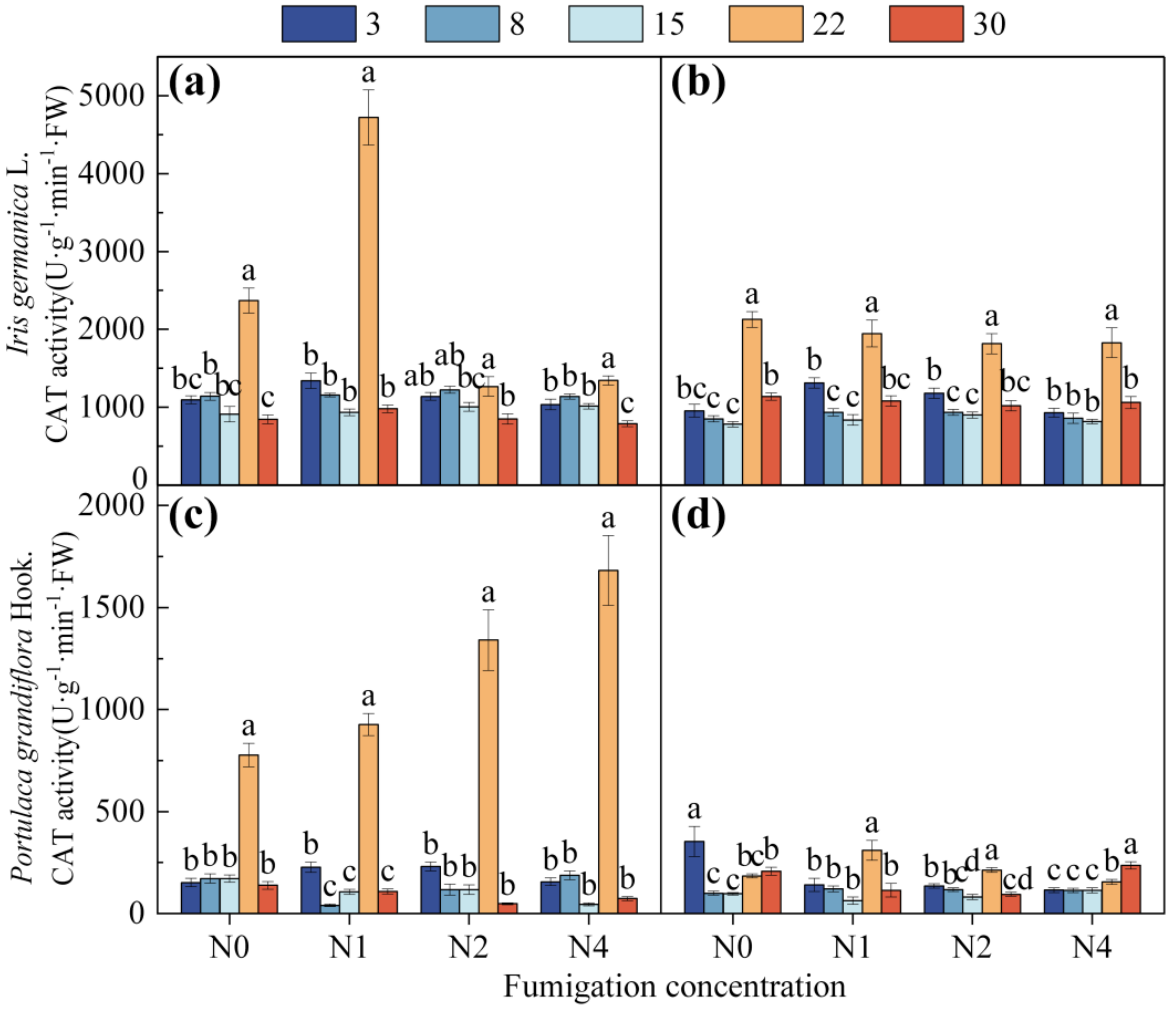


Figure 4. Effect of fumigation time on catalase (CAT) of *Iris germanica* L. and *Portulaca grandiflora* Hook. with different growth stages (n = 8). The error bars are standard errors. (**a**,**c**) represent April (low-growth season), and (**b**,**d**) represent July (high-growth season). Different lowercase letters indicate the significant ($p < 0.05$) difference in CAT activity of plants at the same fumigation concentration and at different fumigation times.

In summary, exposure to inorganic nitrogen-laden $PM_{2.5}$ fumigation influenced the activities of three antioxidant enzymes in *Iris germanica* L. and one antioxidant enzyme in *Portulaca grandiflora* Hook. These results indicated that the response of POD and CAT to different stress levels is more pronounced in *Iris germanica* L. than in *Portulaca grandiflora* Hook.

3.2. Effects of Inorganic Nitrogen-Laden PM on Nitrogen Storage Patterns in Iris germanica L. and Portulaca grandiflora Hook.

In the low-growth season, the nitrogen/weight ratio in the leaves of *Iris germanica* L. exhibited a significant decrease in the N4 treatment compared with that in other treatments. Moreover, the nitrogen/weight ratio in the roots of *Iris germanica* L. notably decreased in the N2 and N4 treatments compared with that in the N0 and N1 treatments. These findings indicated a substantial reduction in the nitrogen/weight ratio of *Iris germanica* L. leaves under high-concentration fumigation treatments, with the nitrogen/weight ratio in roots also decreasing at medium and high concentrations. Conversely, there were no significant differences in the nitrogen/weight ratio of *Portulaca grandiflora* Hook. leaves and roots among all treatments (Figure 6A). Therefore, exposure to $PM_{2.5}$ fumigation containing

inorganic nitrogen resulted in a decrease in the nitrogen/weight ratio in both leaves and roots of *Iris germanica* L., while no such effect was observed in *Portulaca grandiflora* Hook.

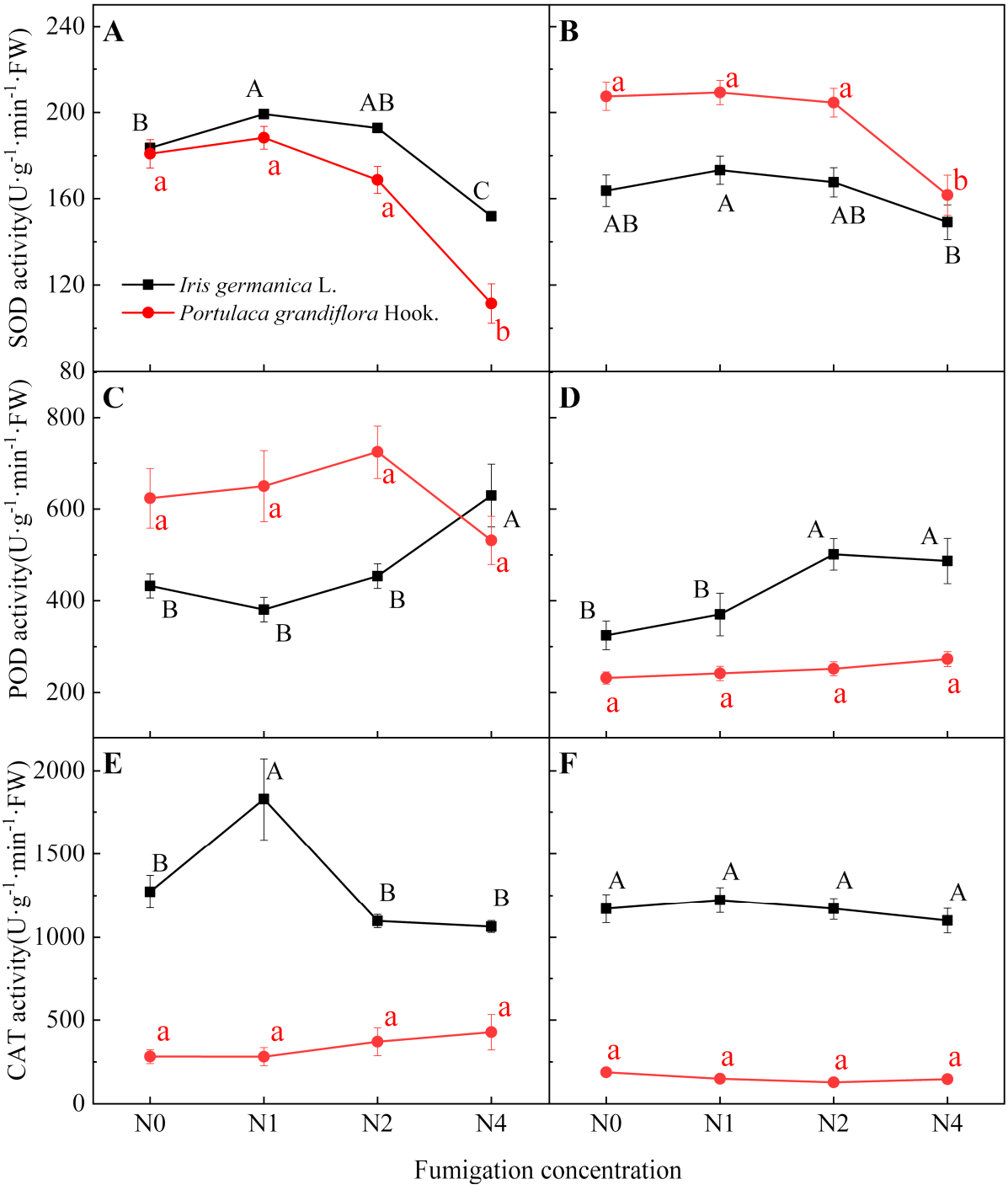


Figure 5. Effects of fumigation concentration on SOD, POD, and CAT in *Iris germanica* L. and *Portulaca grandiflora* Hook. at different growth stages (Duncan's test, $n = 40$, $p < 0.05$). The error bars are standard errors. (**A**,**C**,**E**) represent April (low-growth season), and (**B**,**D**,**F**) represent July (high-growth season). Different uppercase and lowercase letters indicate the significant ($p < 0.05$) difference in three antioxidant enzymes activities (SOD, POD, and CAT) in *Iris germanica* L. and *Portulaca grandiflora* Hook., respectively, under varying fumigation concentrations.

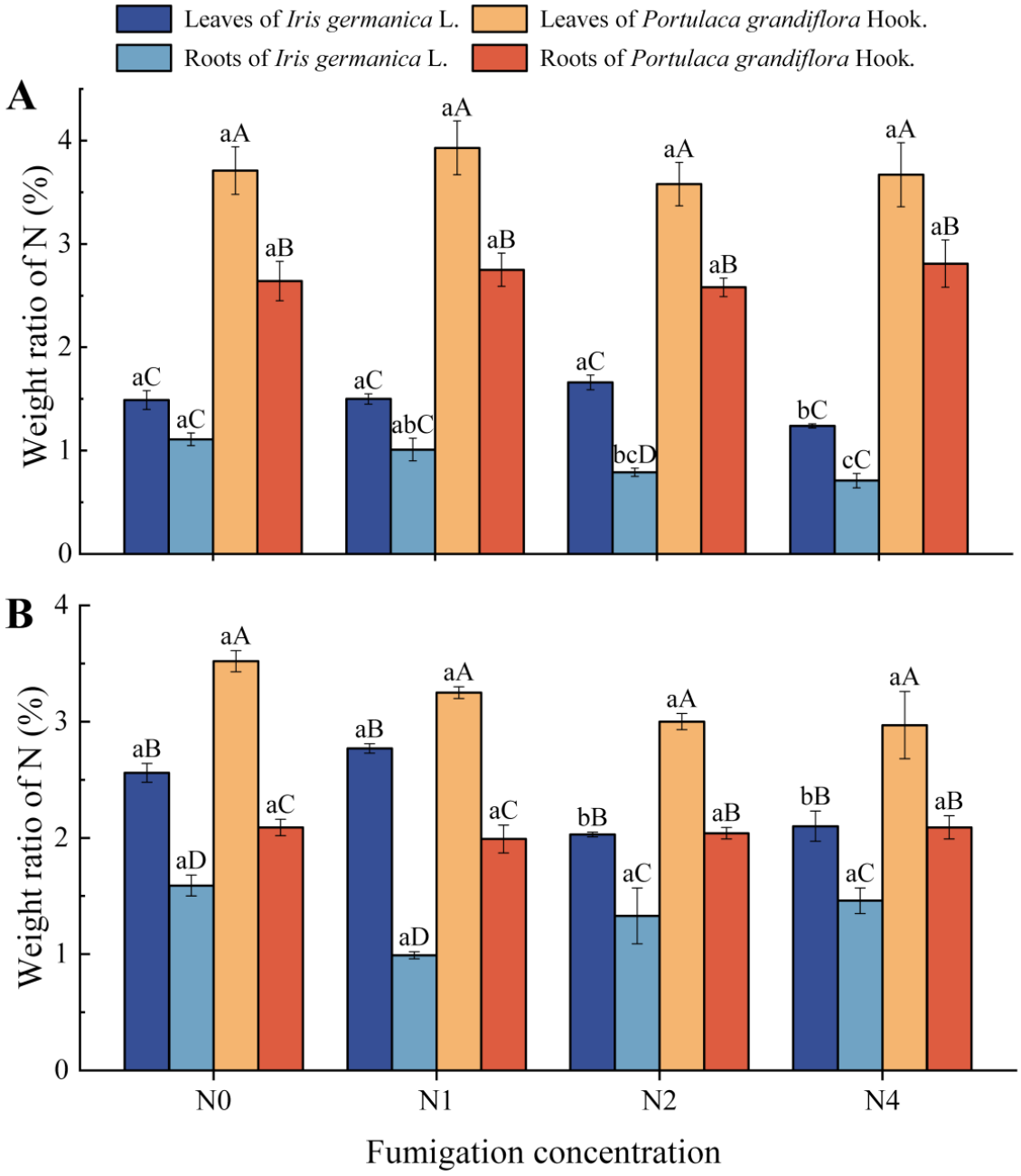


Figure 6. Effects of different growth stages and fumigation concentrations on the weight ratio of N in different organs of *Iris germanica* L. and *Portulaca grandiflora* Hook. (Duncan's test, $n = 4$). The error bars are standard errors. (**A**) represents the low-growth season, and (**B**) represents the high-growth season. In (**A**,**B**), different lowercase letters indicate significant ($p < 0.05$) differences in nitrogen ratios between different concentrations in the same organ of the same plant, and different uppercase letters indicate significant ($p < 0.05$) differences in nitrogen ratios between different organs at the same concentration.

In the high-growth season, the nitrogen/weight ratio in leaves of *Iris germanica* L. was significantly lower in the N2 and N4 treatments compared with that in the N0 and N1 treatments. However, the nitrogen/weight ratio in the roots of *Iris germanica* L., as well as that in the leaves and roots of *Portulaca grandiflora* Hook., showed no significant differences among all treatments ($p > 0.05$). Notably, the nitrogen/weight ratios in the leaves and roots of *Portulaca grandiflora* Hook. were significantly higher than those of *Iris germanica* L. under

all treatment conditions, which indicated a greater nitrogen storage capacity in *Portulaca grandiflora* Hook. cells compared with that in *Iris germanica* L. (Figure 6B).

Overall, the data suggest that heavy PM stress generally results in a decrease in the nitrogen/weight ratio in *Iris germanica* L., whereas no significant reduction in the nitrogen/weight ratio was observed in any parts of *Portulaca grandiflora* Hook. under intense PM stress. This suggests that *Portulaca grandiflora* Hook. demonstrates a superior ability to maintain the nitrogen/weight ratio in vivo under the influence of nitrogen-laden PM stress.

4. Discussion

4.1. Antioxidant Response to Inorganic Nitrogen $PM_{2.5}$ in Iris germanica L. and Portulaca grandiflora Hook.

Under normal physiological conditions, plants maintain a dynamic equilibrium between reactive oxygen species (ROS) production and scavenging. However, adversity stress disrupts this balance by accelerating ROS accumulation [40], triggering the activation of antioxidant enzyme systems to mitigate oxidative damage and sustain growth [41]. Generally, when plants are under mild or moderate adversity stress, the antioxidant system is induced to increase the ability to scavenge ROS; when under severe adversity stress, the balance of the plant's antioxidant system is disrupted and inhibited, and a large amount of ROS accumulates in the body, resulting in organismal damage [42]. The antioxidant system for scavenging reactive oxygen species consists of antioxidant enzymes and antioxidants. The main antioxidant enzymes are SOD, POD, and CAT [43]. Among them, SOD is the fastest reacting indicator of the antioxidant system to eliminate intracellular oxygen ions to form H_2O_2 and O_2 [44], while CAT and POD function to scavenge high intracellular concentrations of hydrogen peroxide [45]. The activity of antioxidant enzymes is closely related to the antioxidant capacity of plants.

Plant antioxidant enzyme systems exhibit differential responses to stress at various growth stages and development phases [46]. In this study, it was observed that two plant antioxidant enzyme systems demonstrated greater stability during the high-growth season, displaying more rapid and persistent responses to stress. Enzymes in plants are normally made up of proteins, and as ambient temperatures rise during the high-growth season, plant photosynthesis increases [47], and the rate of protein production from photosynthesis is faster. This may explain why plant antioxidant enzyme systems demonstrate heightened activity and stability during the high-growth season [48].

In the conducted experiment, the CAT activity of *Iris germanica* L. was notably elevated, whereas the POD activity of *Portulaca grandiflora* Hook. was comparatively heightened. It is worth mentioning that *Iris germanica* L. is categorized as a C3 plant, while *Portulaca grandiflora* Hook. is classified as a C4 plant [35]. The distinction in photosynthesis mechanisms between C3 and C4 plants becomes more pronounced when they are exposed to similar stress stimuli, with C4 plants generally demonstrating higher photosynthetic efficiency compared with that observed in C3 plants [14]. The superior photosynthetic efficiency observed in C4 plants is primarily driven by their capacity to minimize photorespiration, a process that becomes markedly amplified in C3 plants under environmental stress [49]. This adaptive advantage stems from the carbon-concentrating mechanism (CCM), a biochemical strategy that spatially segregates photosynthetic phases to elevate CO_2 concentrations around ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) [50]. By suppressing RuBisCO's oxygenation activity, the CCM effectively enhances carboxylation efficiency, thereby reducing energy losses associated with photorespiration. This not only bolsters photosynthetic performance under optimal conditions but also confers resilience to abiotic stressors such as drought and salinity [51]. Under mild stress conditions, the variance in

antioxidant enzyme profiles between C3 and C4 plants may not be very noticeable. However, a more pronounced disparity in H_2O_2 content emerges under conditions of increased stress intensity. CAT and POD play complementary roles in alleviating environmental stress, with CAT demonstrating superior efficacy in scavenging high concentrations of H_2O_2, while POD excels in scenarios involving lower H_2O_2 concentrations [52]. Moreover, Uzilday et al. [53] observed that the increase in POD activity in C4 plants under drought stress was approximately twofold that of C3 plants, with the highest concentration of H_2O_2 detected in C3 plants based on experimental. This observation helps explain the relatively elevated CAT activity in *Iris germanica* L. and the comparatively heightened POD activity in *Portulaca grandiflora* Hook. during the experiment.

4.2. Nitrogen Storage in Iris germanica L. and Portulaca grandiflora Hook. Under Nitrogen-Laden $PM_{2.5}$ Stress

In this study, the NH_4NO_3 fumigation experiment was utilized to simulate the effects of atmospheric nitrogen deposition via PM originating from NH_4NO_3 solution, which can infiltrate plants through the stomata of leaves [54,55] or permeate the plant surface [56]. Inorganic nitrogenous salts enter the plant system, initially being absorbed and transported by the plant and subsequently transforming into organic nitrogen through assimilation [57].

In most experiments, heightened nitrogen-laden PM stress levels have been linked to a decrease in the nitrogen/weight ratio in plants. Generally, as the external nitrogen availability increases, the plant nitrogen/weight ratio tends to elevate [58]. Optimal increases in nitrogen levels can enhance plant N-assimilating enzyme activities [59], while excessively high nitrogen levels may lead to reduced activities of certain N-assimilating enzymes [60], resulting in decreased plant nitrogen content and affect carbon and nitrogen balance in plants [61]. Several studies have documented nitrogen loss from aboveground plant parts upon excessive fertilizer application [62–65], frequently attributed to nitrogen translocation from aboveground to roots or soil (e.g., nitrate leaching), leaching from leaves, and emission into the atmosphere as gases (e.g., N_2O). By contrast, the nitrogen/weight ratio of *Portulaca grandiflora* Hook. exhibited no significant decrease under severe conditions. This resilience to inorganic nitrogen-laden fumigation in *Portulaca grandiflora* Hook. suggests a less pronounced response compared to that of *Iris germanica* L. Building on our research group's previous experimental work with *Portulaca grandiflora* Hook. [35], demonstrate that the species employs a compensatory 'over-photosynthesis' mechanism to counteract reduced leaf nitrogen mass. Fumigation of nitrogen-laden $PM_{2.5}$ stimulated an increase in stomatal conductance [66,67], contributing to an increase in nitrogen influx through the pores and the sub-pores [68]. This resulted in a temporary but large increase in nitrogen concentration in the gas exchange space in direct contact with chloroplasts. This plasticity of nitrogen storage under $PM_{2.5}$ stress is consistent with the adaptive strategies of *Portulaca grandiflora* Hook. to salinity. Under salinity stress (400 mM NaCl), *Portulaca grandiflora* Hook. maintains nitrogen assimilation efficiency through sustained K^+ transport from roots to leaves, stabilizing ion homeostasis and minimizing oxidative damage [31]. In contrast, *Iris germanica* L. exhibits severe inhibition of nitrogen uptake at 100 mM NaCl, associated with ROS accumulation and reduced SOD activity [69]. These findings highlight that stress tolerance mechanisms are stressor-specific, while *Portulaca grandiflora* Hook. leverages ion transport for salinity and metabolic plasticity for $PM_{2.5}$, *Iris germanica* L.'s sensitivity across stressors stems from its limited antioxidant redundancy and C3 metabolic constraints.

After a month of continuous fumigation with fine PM containing inorganic nitrogen, the results revealed a significantly higher N ratio in all organs of *Portulaca grandiflora* Hook. compared with that in *Iris germanica* L. *Portulaca grandiflora* Hook. may use its higher nitrogen uptake and utilization capacity to convert more inorganic nitrogen into organic nitrogen and store it in its organs, thus responding to stress by increasing nitrogen accu-

mulation, whereas *Iris germanica* L. may have relatively low nitrogen levels in its organs due to growth restriction or impaired nitrogen metabolism. Morphologically, the main assimilation process of NO_3^- uptake in herbaceous plants mainly occurs in the chloroplasts, the leaf mesophyll cells of the C4 plant *Portulaca grandiflora* Hook. exhibit larger and more numerous chloroplasts, in contrast to the smaller vascular sheath cells lacking chloroplasts in the C3 plant *Iris germanica* L. [70]. Furthermore, enzymes related to nitrogen absorption are predominantly located in the chloroplasts of leaf mesophyll cells [71]. The abundant and large chloroplasts in *Portulaca grandiflora* Hook. enhance its nitrogen assimilation efficiency, supported by the C4 plant-specific pathway, maintaining increased photosynthetic efficiency and carbon assimilation rates at lower CO_2 concentrations [72], thereby augmenting nitrogen uptake and storage capacity [73].

5. Conclusions

Significant disparities in the antioxidant defense mechanisms utilized by *Iris germanica* L. and *Portulaca grandiflora* Hook. when confronted with nitrogen-laden PM stress. *Iris germanica* L. primarily employed CAT to mitigate reactive oxygen species, specifically H_2O_2, whereas *Portulaca grandiflora* Hook. primarily depended on POD for H_2O_2 scavenging. Moreover, *Portulaca grandiflora* Hook. demonstrated superior preservation of enzyme activities under extended fumigation treatments compared with that in *Iris germanica* L., indicating a more robust and sustained response to stress. The plant antioxidant enzyme systems exhibited enhanced consistency throughout the high-growth season and responses to stress in both species. The differing adaptive mechanisms employed by *Iris germanica* L. and *Portulaca grandiflora* Hook. in response to excess nitrogen led to the observation that severe particulate stress often resulted in decreased nitrogen/weight ratios in *Iris germanica* L., while *Portulaca grandiflora* Hook. showed no significant decrease in nitrogen ratios under similar stress conditions. Furthermore, *Portulaca grandiflora* Hook. demonstrated an ability to adapt to elevated ambient nitrogen concentrations, allowing for moderate nitrogen accumulation within its tissues, thereby enhancing its nitrogen storage capacity. In conclusion, this study confirms that *Portulaca grandiflora* Hook. exhibited greater resilience to stress throughout the high-growth season, underscoring its superior capacity to withstand the adverse effects of elevated nitrogen deposition and particulate pollution. Our study provides a clearer understanding of the plant response to pollution, as well as theoretical support for future plant screening. Specifically, the robust antioxidant defense system and nitrogen storage capacity of *Portulaca grandiflora* Hook. suggest its potential as a priority species for green infrastructure in nitrogen-polluted environments, such as industrial zones or traffic-dense urban areas. Future research should explore the scalability of these adaptive traits under field conditions, including long-term monitoring of nitrogen accumulation dynamics and interactions with other environmental stressors (e.g., heavy metals).

Author Contributions: Conceptualization, S.P., Z.G. and Z.M.; methodology, K.X.; validation, S.P.; formal analysis, K.X., Y.W., R.W. and Z.H.; investigation, K.X., Y.W., R.W. and Z.H.; resources, Z.G. and Z.M.; data curation, Z.G. and Z.M.; writing—original draft, K.X.; writing—review and editing, K.X.; visualization, Y.W., R.W. and Z.H.; supervision, S.P., Z.G. and Z.M.; project administration, Z.G. and Z.M.; funding acquisition, S.P., Z.G. and Z.M. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Jiangsu Forestry Science & Technology Innovation and Extension Project (Project No: LYKJ [2022]02 & LYKJ [2022]16), Jiangsu Social Development Project (BE2022792), the National Natural Science Foundation of China (grant numbers 31870506, 32271712).

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors upon request.

Conflicts of Interest: The authors declare no conflicts of interest.

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