

# Is the Invasive Plant *Amaranthus spinosus* L. More Competitive than the Native Plant *A. tricolor* L. When Exposed to Acid Deposition with Different Sulfur–Nitrogen Ratios?

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**Abstract:** The functional differences between invasive plants and coexisting native plants can affect the invasion process of the former because invasive plants and coexisting native plants are exposed to similar or even identical environmental pressures. Acid deposition is an important component of atmospheric pollution, and acid deposition with different sulfur–nitrogen ratios may affect the invasion process of invasive plants by shifting the functional differences and differences in the growth performance between the invasive and coexisting native plants. It is crucial to analyze the functional indices and growth performance of these plants when exposed to acid deposition with different chemical compositions to assess the ecological impacts of atmospheric pollution on the growth performance of invasive plants. This study aimed to evaluate the functional differences and growth performance between the invasive plant *Amaranthus spinosus* L. and the native plant *A. tricolor* L. in mono- and mixed culture when exposed to an acid deposition with different sulfur–nitrogen ratios, including sulfur-rich acid deposition (sulfur–nitrogen ratio = 5:1), nitrogen-rich acid deposition (sulfur–nitrogen ratio = 1:5), and mixed acid deposition (sulfur–nitrogen ratio = 1:1). The acidity of the three types of simulated acid deposition was set at pH = 5.6 and pH = 4.5, respectively, with distilled water as a control (pH = 7.0). The competition experiment between *A. spinosus* and *A. tricolor* was conducted in the greenhouse. *Amaranthus spinosus* exhibited a strong growth performance over *A. tricolor* in the mixed culture, mainly via the increased leaf photosynthetic capacity. The competitiveness for light acquisition, leaf photosynthetic capacity, and enzymatic defense capacity under stress of *A. spinosus* may be vital to its growth performance. The lower pH acid deposition had imposed a greater reduction in the growth performance of both *Amaranthus* species than the higher pH acid deposition. Sulfur-rich acid deposition was more toxic to the growth performance of both *Amaranthus* species than nitrogen-rich acid deposition. *Amaranthus spinosus* was more competitive than *A. tricolor*, especially when exposed to acid deposition, compared with just distilled water. Thus, acid deposition, regardless of the sulfur–nitrogen ratio, may facilitate the invasion process of *A. spinosus* via the stronger growth performance.

**Keywords:** functional difference; growth performance; invasion process; nitrogen-rich acid deposition; sulfur-rich acid deposition



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## 1. Introduction

Invasive plants pose a significant threat to ecological stability because they can lead to changes in community function and biodiversity loss [1–3]. Therefore, the study of the mechanism by which invasion occurs is one of the hot topics in invasion ecology research in recent years [4–6].

The functional differences between invasive plants and coexisting native plants regulate whether the former can successfully invade, as invasive and coexisting native plants both suffer from similar or even the same selection pressures imposed by their environment [7–9]. In general, invasive plants have a higher growth performance than coexisting native plants due to higher values of key functional traits [7,8,10]. Therefore, it is imperative to elucidate the functional differences and differences in the growth performance-related traits between invasive and coexisting native plants to shed light on the mechanisms underlying the successful invasion of invasive plants.

Acid deposition is an important component of atmospheric pollution and can significantly affect ecological functions, such as the growth performance of plant species [11–13]. Acid deposition can also affect the invasion process of invasive plants, especially by altering their growth performance and allelopathic intensity [11,14,15]. China is one of the three regions in the world most severely affected by acid deposition [16–18], and the type of acid deposition in China has changed from sulfur-rich acid deposition to mixed sulfur and nitrogen acid deposition and, more recently, to nitrogen-rich acid deposition [14,19,20]. In other words, the sulfur–nitrogen ratio in the rain in China is gradually decreasing, mainly due to the recent adjustments in the energy structure and energy-related policies [14,19,20]. Changes in the composition of acid deposition may alter the ability of invasive plants to invade new habitats. Therefore, it is crucial to improve our understanding of the functional differences and differences in the growth performance between invasive and coexisting native plants when exposed to different compositions of acid deposition to explain the mechanisms driving the successful habitat invasion by invasive plants under various acid deposition scenarios. However, little progress has been made in this area so far.

This study aimed to estimate the functional differences and differences in the growth performance between the invasive plant *Amaranthus spinosus* L. (spiny amaranth) and the native plant *A. tricolor* L. (red amaranth) in mono- and mixed culture and when exposed to acid deposition composed of different sulfur–nitrogen ratios, including sulfur-rich acid deposition (sulfur–nitrogen ratio = 5:1), nitrogen-rich acid deposition (sulfur–nitrogen ratio = 1:5), and mixed acid deposition (sulfur–nitrogen ratio = 1:1). Both *Amaranthus* species can coexist in the same habitat, such as wasteland and farmland, in East China [10,21]. In East China, the number of invasive *Amaranthus* species is significantly higher than among other genera, and there are currently 16 species of invasive plants belonging to *Amaranthus*, which accounts for about 5.35% of the total number of invasive plant species in the region [22]. As a spiny annual or perennial herb, *A. spinosus* is native to tropical America and has had a significant impact on non-native ecosystems [23–25]. The area in China where *A. spinosus* has invaded (including East China) and is currently also experiencing severe acid deposition [14,19,20].

This study tested the following hypotheses: (I) acid deposition can reduce the growth performance of both *Amaranthus* species, and the effects of acid deposition vary with different sulfur–nitrogen ratios, and (II) *A. spinosus* may be more competitive than *A. tricolor* when exposed to acid deposition regardless of the sulfur–nitrogen ratios.

## 2. Materials and Methods

### 2.1. Experimental Design

The competition experiment between *A. spinosus* (seeds collected at 32.113° N, 119.532° E, Zhenjiang, Jiangsu, East China) and *A. tricolor* cv. xinbai (manufacturer: Qingxian Chunfeng Vegetable Cultivars Breeding Base, Hebei, China) was conducted in planting pots. The culture matrix was composed of pre-sterilized store-bought pasture soil (pH value:  $\approx 6.5$ ; organic content:  $\geq 40\%$ ; produced by Jiangsu Zhongfang Agriculture and Pastoral Hus-

bandry Co. LTD) to avoid using soil collected from the field, which may be infested with invasive plants or contaminated by acid rain.

Six vigorous seedlings with uniform height belonging to the two *Amaranthus* species were planted in each planting pot (upper diameter:  $\approx 25$  cm). The planting pattern was as follows: (I) monoculture of *A. spinosus* with six seedlings, (II) monoculture of *A. tricolor* with six seedlings, and (III) mixed culture of *A. spinosus* and *A. tricolor* with three seedlings per species.

The seedlings were exposed to three types of acid deposition: (I) sulfur-rich acid deposition (sulfur–nitrogen ratio = 5:1), (II) nitrogen-rich acid deposition (sulfur–nitrogen ratio = 1:5), and (III) mixed acid deposition (sulfur–nitrogen ratio = 1:1). The three acid deposition scenarios were created by mixing  $0.5 \text{ M L}^{-1} \text{ H}_2\text{SO}_4$  and  $0.5 \text{ M L}^{-1} \text{ HNO}_3$  at different ratios. The acidity of the three acid deposition types was set to pH = 5.6 and pH = 4.5, respectively. In particular, (I)  $\text{SO}_4^{2-}$  and  $\text{NO}_3^-$  are the main components of natural acid precipitation in the study area, (II) the acidity of normal unpolluted precipitation is almost 5.6, (III) the acidity of natural acid precipitation in the study area is about 4.5, and (IV) the sulfur–nitrogen ratio of natural acid precipitation in the study area is about 5:1 [14,19,20]. Distilled water was used as a control (pH = 7.0). Three planting pots were used per treatment.

The seedlings were grown in a greenhouse at Jiangsu University, Zhenjiang, Jiangsu, East China (located at  $32.206^\circ \text{ N}$ ,  $119.512^\circ \text{ E}$ ) under natural light conditions for 50 d. The climate type of the study area is a subtropical monsoon wet climate (mean annual hours of sunshine  $\approx 1996.8 \text{ h}$ ; mean annual precipitation  $\approx 1101.4 \text{ mm}$ , and mean annual temperature  $\approx 15.9^\circ \text{ C}$ ) [26].

After 50 d of experimental treatment, all individuals of the two *Amaranthus* species were collected to estimate their functional indices, biochemical constituents, and osmolytes indices.

## 2.2. Determination of the Functional Indices, and Biochemical Constituents and Osmolytes Indices of the Two *Amaranthus* Species

The functional indices of the two *Amaranthus* species included (I) plant height (representing the competitiveness for sunlight acquisition), (II) ground diameter (representing plant supporting ability), (III) leaf size (characterized as leaf length and width, representing leaf photosynthetic area), (IV) green leaf area (representing leaf photosynthetic area), (V) leaf thickness (representing leaf supporting ability), (VI) single-leaf wet and dry weights (representing leaf growing competitiveness), (VII) leaf water content (representing leaf moisture content), (VIII) specific leaf area (representing leaf resource use efficiency and acquisition capacity), (IX) leaf chlorophyll and nitrogen concentrations (representing leaf photosynthetic capacity), (X) plant aboveground wet and dry weights (representing aboveground growing competitiveness), and (XI) plant aboveground water content (representing aboveground moisture content). The procedures used to determine the functional indices are described in our previous study [27,28].

The biochemical constituents and osmolytes indices of the two *Amaranthus* species included (I) plant malondialdehyde content (representing the level of peroxidation of the cytoplasm membrane under stress; measured using the thiobarbituric acid method with spectrophotometry (model: uv-2450; manufacturer: Shimadzu, Kyoto, Japan; the same as below) at 532 nm), (II) plant proline content (representing the level of osmotic adjustment capacity under stress; measured using the acidic ninhydrin method with spectrophotometry at 520 nm), (III) plant soluble sugar content (representing the level of osmotic adjustment capacity under stress; measured using the thiobarbituric acid method with spectrophotometry at 450 nm), (IV) plant catalase activity (EC 1.11.1.6; representing enzymatic defense capacity under stress specifically to oxidative stress; measured using the  $\text{H}_2\text{O}_2$  method with spectrophotometry at 240 nm), (V) plant peroxidase activity (EC 1.11.1.7; representing enzymatic defense capacity under stress specifically to oxidative stress; measured using the guaiacol method with spectrophotometry at 470 nm), and

(VI) plant superoxide dismutase activity (EC 1.15.1.1; representing enzymatic defense capacity under stress specifically to oxidative stress; measured using the nitro-blue tetrazolium method with spectrophotometry at 560 nm) [29–32].

The growth performance of *A. spinosus* was evaluated using the relative dominance index. The value of the relative dominance index was evaluated using the ratio of *A. spinosus*' biomass in the mixed culture to the sum of *A. spinosus*' biomass and *A. tricolor*'s biomass in the mixed culture [6,33,34].

### 2.3. Statistical Analysis

The differences among the treatments were assessed using the one-way analysis of variance (ANOVA) and Tukey HSD. Four-way ANOVA was used to assess the effects of planting pattern, plant species, acid deposition acidity, acid deposition type, and their interactions on the evaluated variances. Partial Eta-squared ( $\eta^2$ ) was also estimated to assess the effect size of each factor used in the four-way ANOVA.  $p \leq 0.05$  was considered to represent a statistically significant difference. Statistical analyses were performed using IBM SPSS Statistics 26.0.

### 3. Results and Discussion

The growth performance of the two *Amaranthus* species may be reduced in the mixed culture compared with the monoculture mainly due to the limited resources available resulting from the increased interspecific competition in the mixed culture [11,35,36]. As expected, the leaf photosynthetic capacity of *A. tricolor* in the mixed culture was 20.59% lower than that in the monoculture when exposed to the mixed acid deposition at pH 4.5 ( $p < 0.05$ ; Figure 1). Thus, the growth performance of *A. tricolor* in the mixed culture may be reduced largely via the decreased leaf photosynthetic capacity. However, the leaf photosynthetic capacity of *A. spinosus* in the mixed culture was  $\approx 10.87\%$  higher than that in the monoculture in all treatments (except nitrogen-rich acid at pH 5.6) ( $p < 0.05$ ; Figure 1). Thus, the growth performance of *A. spinosus* may be increased in the mixed culture chiefly via the increased leaf photosynthetic capacity. Moreover, the leaf photosynthetic capacity of *A. spinosus* was  $\approx 34.99\%$  higher than that of *A. tricolor* in all treatments regardless of planting pattern ( $p < 0.05$ ; Figure 1). Thus, *A. spinosus* exhibited a strong growth performance over *A. tricolor* in the mixed culture mainly due to the enhanced leaf photosynthetic capacity [11,28,37]. Hence, the leaf photosynthetic capacity of *A. spinosus* may be vital to its growth performance, especially in the mixed culture. In addition, the four-way ANOVA results also showed that the planting pattern significantly affected the leaf photosynthetic capacity of the two *Amaranthus* species ( $p < 0.05$ ; Table S1).

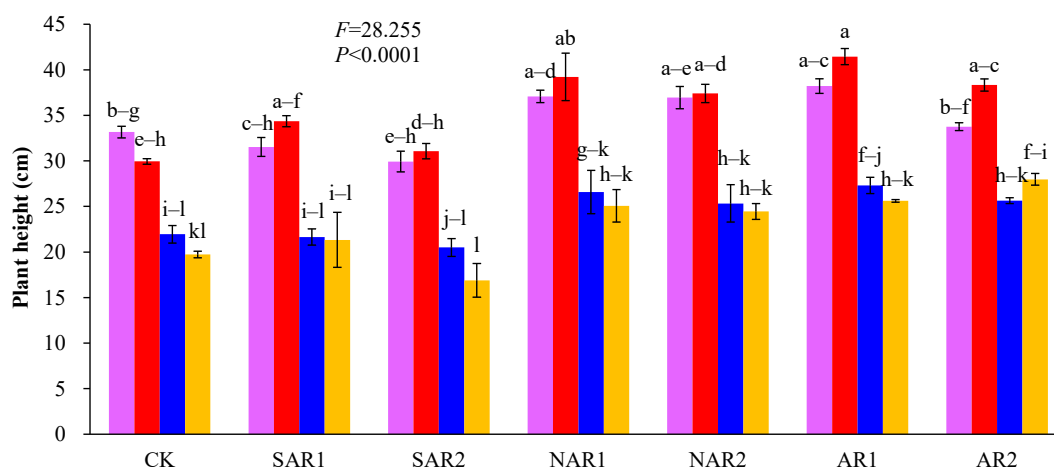


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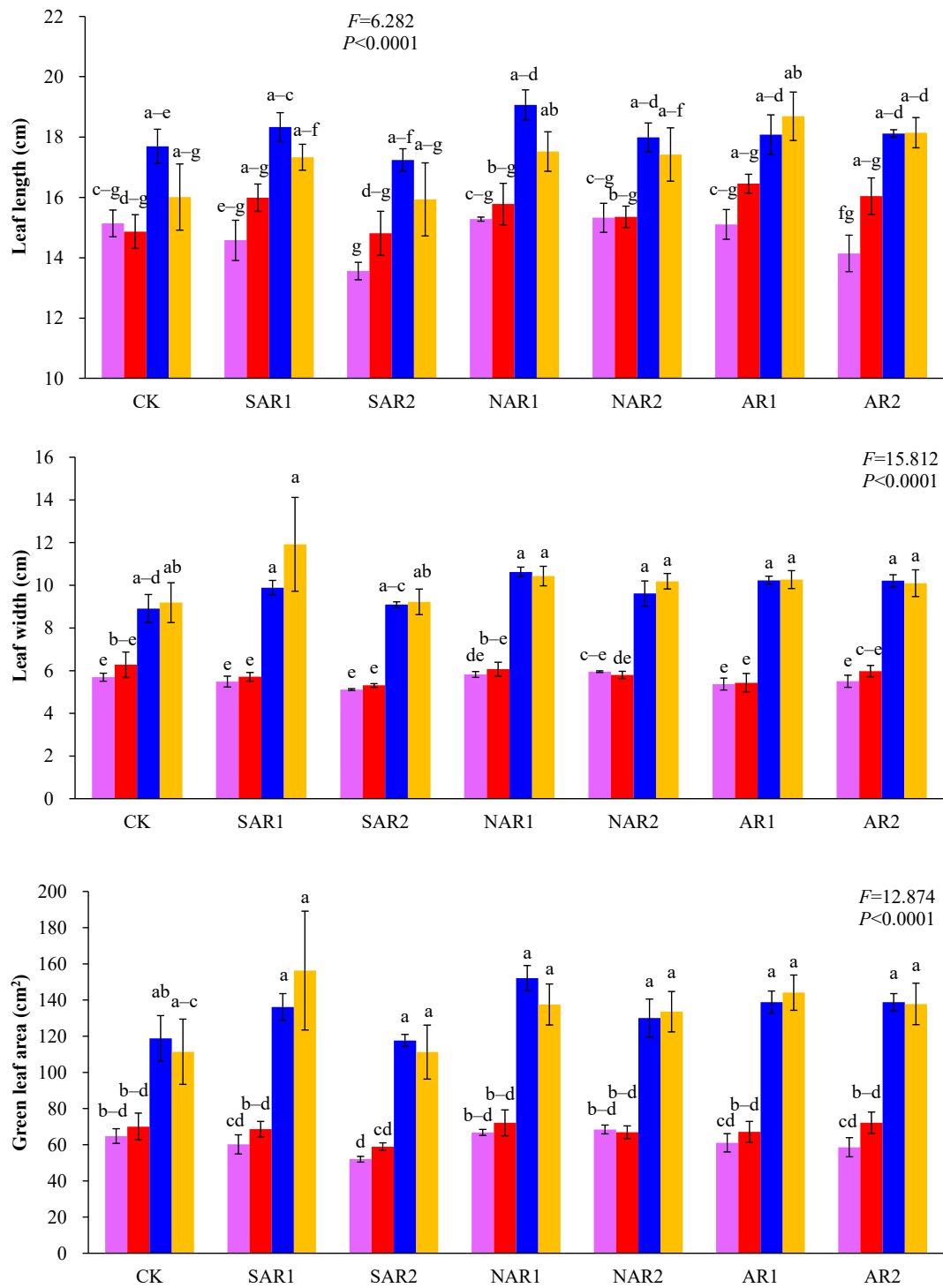


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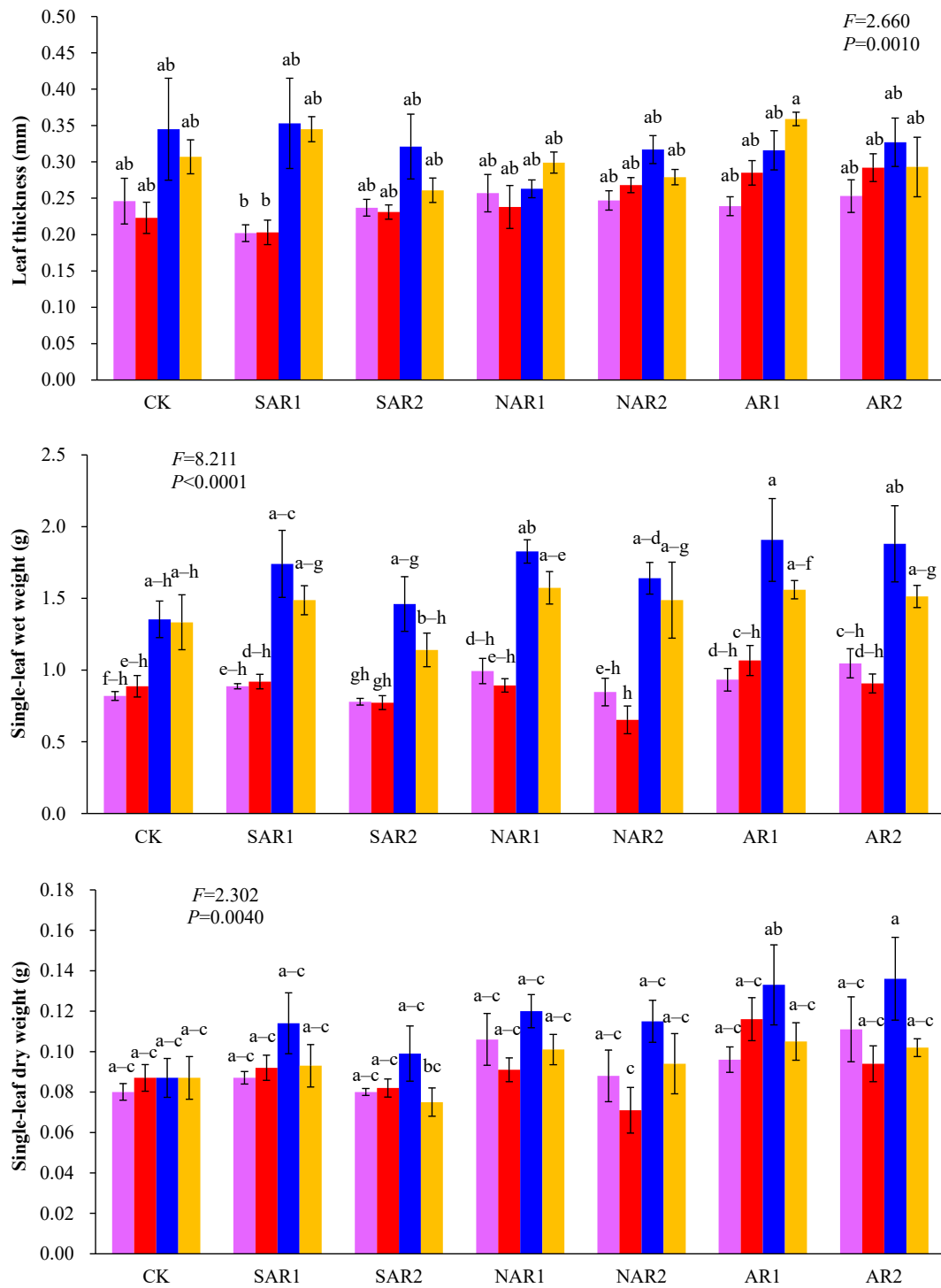


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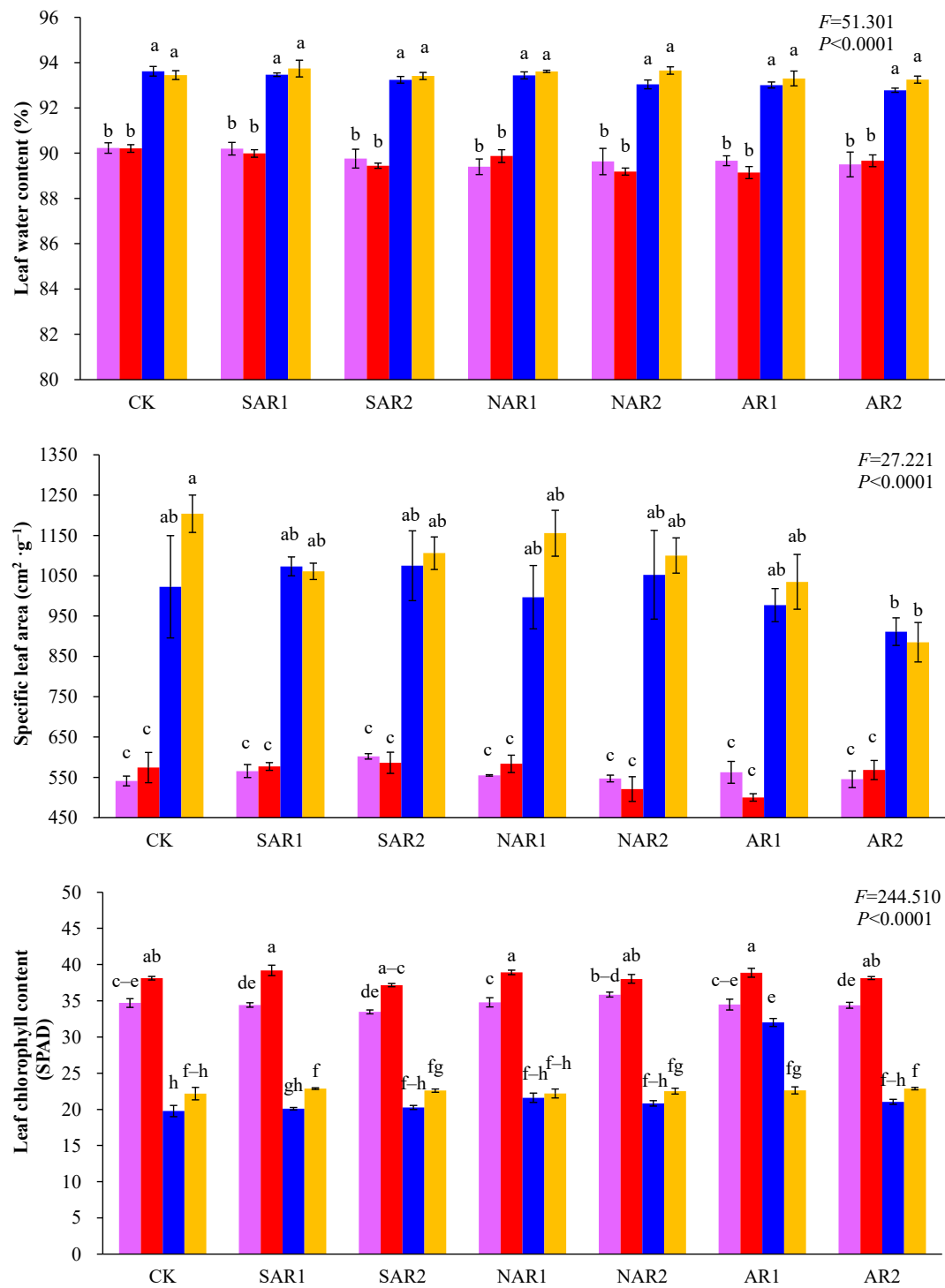
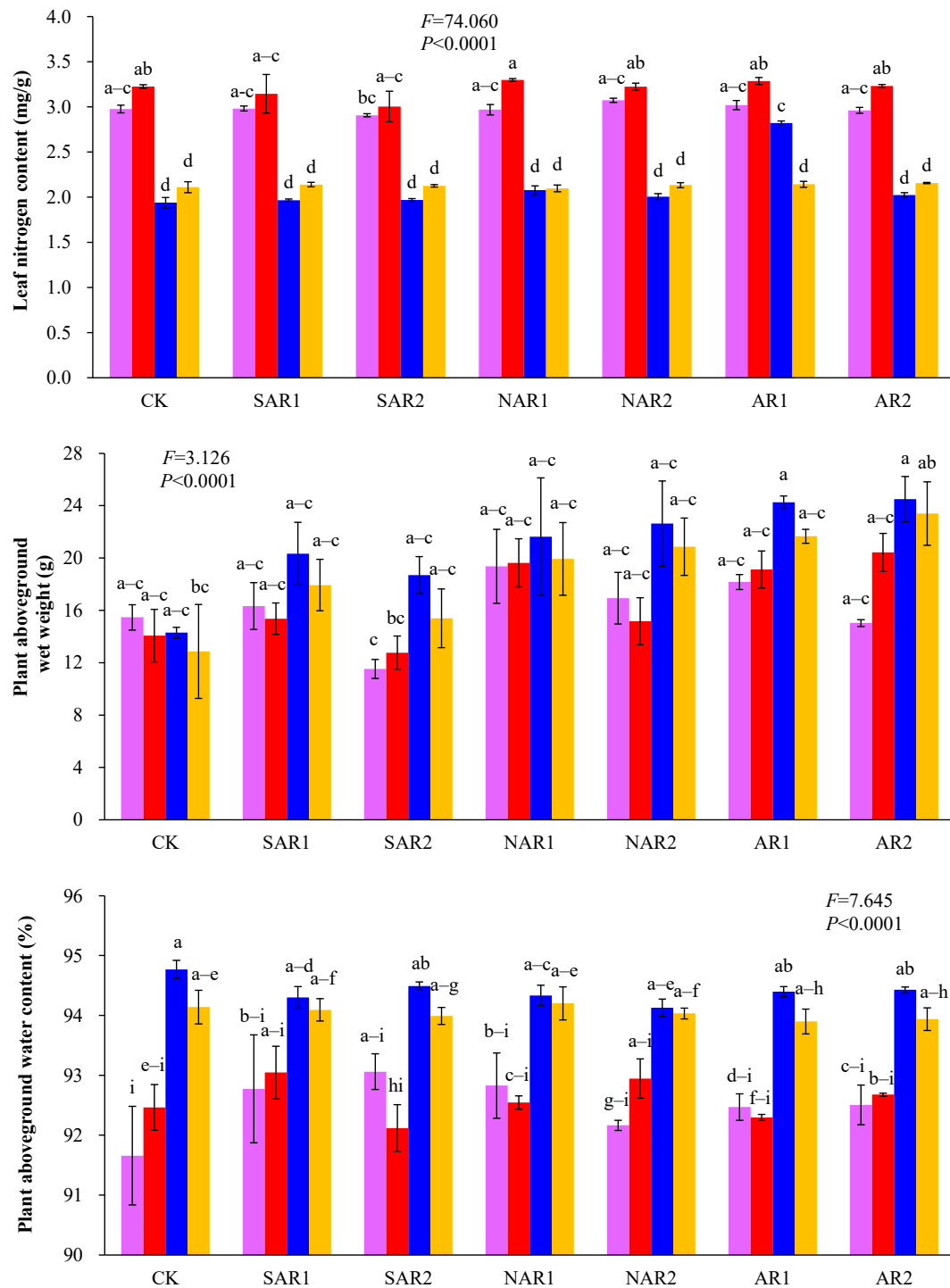


Figure 1. Cont.



**Figure 1.** Morphological and physiological indices of *Amaranthus spinosus* and *A. tricolor* in mono- and mixed culture (monoculture *A. spinosus*, purple bars; mixed culture *A. spinosus*, red bars; monoculture *A. tricolor*, blue bars; mixed culture *A. tricolor*, orange bars). Bars (mean with standard error,  $n = 3$ ) with different lowercase letters indicate statistically significant differences ( $p \leq 0.05$ ). The two indices (i.e., ground diameter and plant aboveground dry weight) with no statistically significant difference ( $p > 0.05$ ) among all treatments are not shown in this figure. Abbreviations: CK, control (distilled water; pH = 7.0); SAR1, sulfur-rich acid deposition (sulfur–nitrogen = 5:1; pH = 4.5); SAR2, sulfur-rich acid deposition (sulfur–nitrogen = 5:1; pH = 5.6); NAR1, nitrogen-rich acid deposition (sulfur–nitrogen = 1:5; pH = 4.5); NAR2, nitrogen-rich acid deposition (sulfur–nitrogen = 1:5; pH = 5.6); AR1, mixed acid deposition (sulfur–nitrogen = 1:1; pH = 4.5); AR2, mixed acid deposition (sulfur–nitrogen = 1:1; pH = 5.6).



Usually, the values of the key functional traits of invasive plants are higher than those of the coexisting native plants [8,10,11]. In this study, the competitiveness for light acquisition and leaf photosynthetic capacity of *A. spinosus* were  $\approx 32.98\%$  and  $\approx 34.99\%$  higher than those of *A. tricolor* in all treatments, respectively ( $p < 0.05$ ; Figure 1). The enzymatic defense capacity under stress of *A. spinosus* was also higher than in *A. tricolor* when exposed to nitrogen-rich acid deposition ( $p < 0.05$ ; Figure 2). Therefore, the competitiveness for light acquisition, leaf photosynthetic capacity, and enzymatic defense capacity under stress in *A. spinosus* may be critical to its growth performance, especially when exposed to acid deposition. In addition, the four-way ANOVA results showed that the plant species significantly affected the competitiveness for light acquisition, leaf photosynthetic capacity, and enzymatic defense capacity under stress of the two *Amaranthus* species ( $p < 0.05$ ; Table S1). However, the leaf photosynthetic area, leaf growing competitiveness, leaf moisture content, leaf resource use efficiency, and acquisition capacity, and aboveground moisture content of *A. spinosus* were lower than those of *A. tricolor* under partial treatments ( $p < 0.05$ ; Figures 1 and 2), which suggests that this latter list of functional indices may not be important to the growth performance of *A. spinosus*. Thus, *A. spinosus* may be gaining a higher growth performance by enhancing certain key ecological functions, such as the competitiveness for light acquisition, leaf photosynthetic capacity, and enzymatic defense capacity under stress.

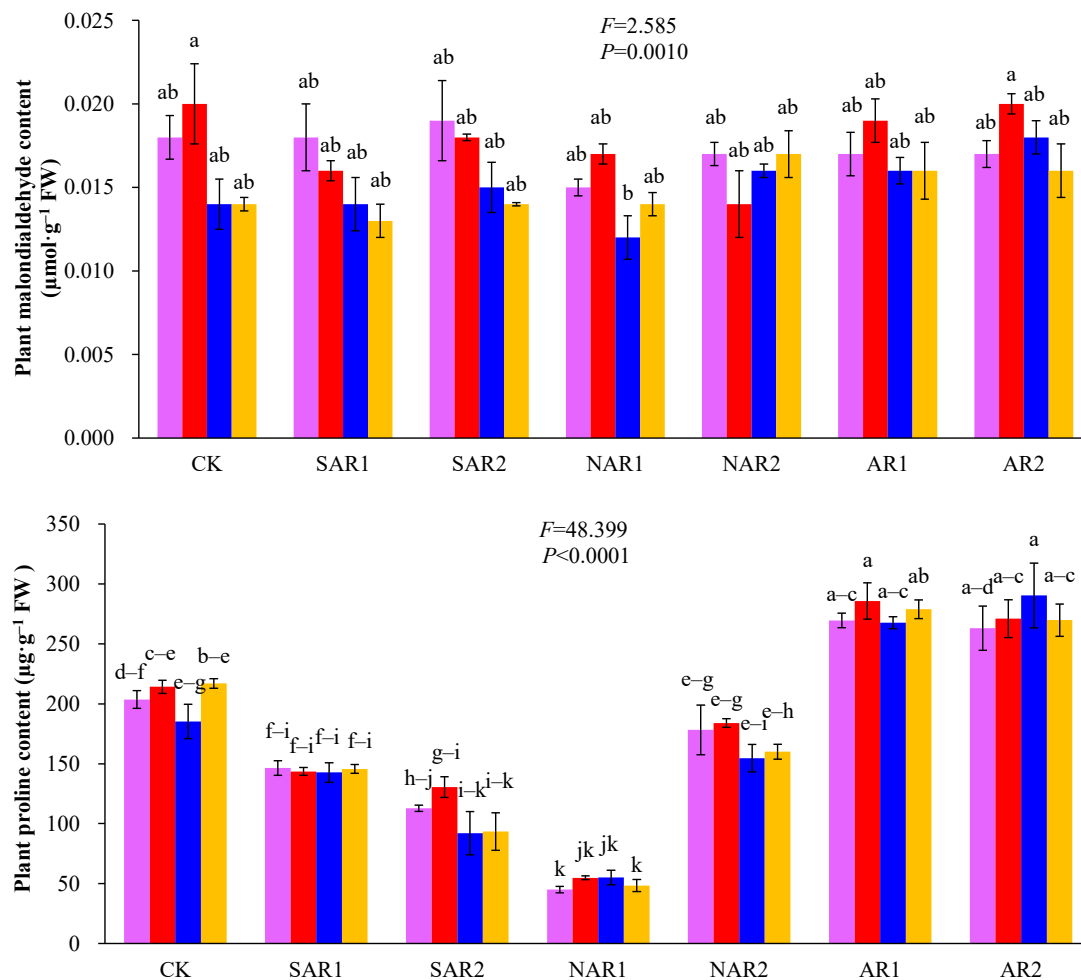
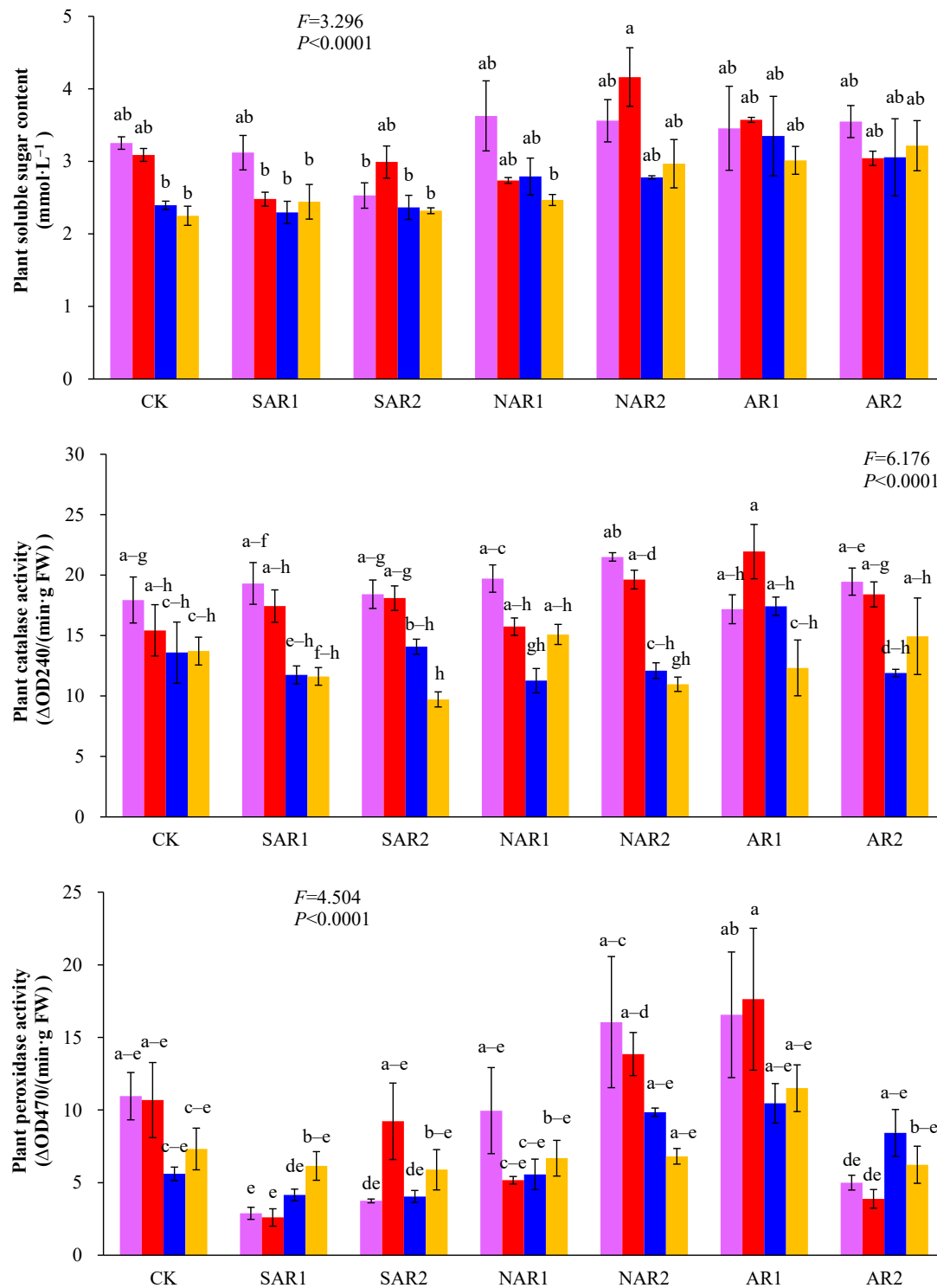


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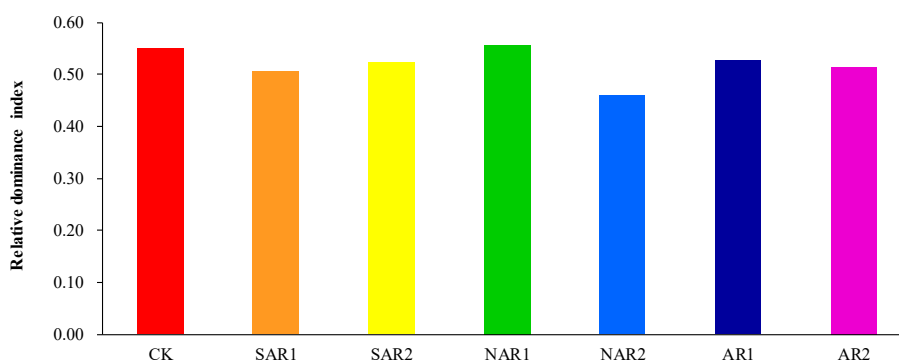
**Figure 2.** Biochemical constituents and osmolytes indices of *Amaranthus spinosus* and *A. tricolor* in mono- and mixed culture (monoculture *A. spinosus*, purple bars; mixed culture *A. spinosus*, red bars; monoculture *A. tricolor*, blue bars; mixed culture *A. tricolor*, orange bars). Bars (mean with standard error,  $n = 3$ ) with different lowercase letters indicate statistically significant differences ( $p \leq 0.05$ ). The index (i.e., plant superoxide dismutase activity) with no statistically significant difference ( $p > 0.05$ ) across all treatments is not shown in this figure. Abbreviations have the same meanings as presented in Figure 1.

Acid deposition can reduce the growth performance of plant species [11–13]. In this study, the acidity and composition of the acid deposition were two major factors

affecting the growth performance of the two *Amaranthus* species (Figures 1 and 2; Table S1). The osmotic adjustment capacity under stress of the two *Amaranthus* species exposed to nitrogen-rich acid deposition at pH 4.5 was lower than when exposed to nitrogen-rich acid deposition at pH 5.6 ( $p < 0.05$ ; Figure 2). Thus, the lower pH acid deposition may be more toxic to the growth performance of both *Amaranthus* species than the higher pH acid deposition because the lower pH acid deposition, especially given that more hydrogen ions may be released, may induce a more intense stress response potentially through enhanced nutrient leaching [11,14,38]. In addition, four-way ANOVA results showed that the acid deposition acidity significantly affected the osmotic adjustment capacity under stress of the two *Amaranthus* species ( $p < 0.05$ ; Table S1).

The main components of acid deposition are  $\text{SO}_4^{2-}$  and  $\text{NO}_3^-$ , and acid deposition with different sulfur–nitrogen ratios can affect the growth performance of plant species [14,38,39]. In this study, sulfur-rich acid deposition caused a greater reduction in the competitiveness for light acquisition and leaf photosynthetic capacity of the two *Amaranthus* species than nitrogen-rich acid deposition ( $p < 0.05$ ; Figure 1). This phenomenon may be due to the higher nitrogen content in nitrogen-rich acid deposition than in sulfur-rich acid deposition. Since nitrogen is one of the essential nutrients required for the growth performance of plants (i.e., fertilization effect), a nitrogen-rich deposition may actually provide some nutrient relief, albeit at the expense of soil acidification [14,38,39]. The two *Amaranthus* species also exhibited a higher level of osmotic adjustment capacity when exposed to sulfur-rich acid deposition than when exposed to nitrogen-rich acid deposition ( $p < 0.05$ ; Figure 2). Thus, sulfur-rich acid deposition exerted a greater negative impact on the growth performance of the two *Amaranthus* species than nitrogen-rich acid deposition [14,40,41], and this result supports the first hypothesis. In addition, four-way ANOVA results showed that the acid deposition composition significantly affected the competitiveness for light acquisition, the leaf photosynthetic capacity, and the osmotic adjustment capacity of the two *Amaranthus* species ( $p < 0.05$ ; Table S1).

The relative dominance index of *A. spinosus* in this study was higher than 0.5 in all acid deposition treatments (average: 0.5286) except in the nitrogen-rich acid deposition treatment at pH 5.6 (Figure 3). Thus, *A. spinosus* exhibited a higher growth performance than *A. tricolor*, especially when exposed to acid deposition with different sulfur–nitrogen ratios. Therefore, acid deposition, regardless of the sulfur–nitrogen ratio, may accelerate the invasion process of *A. spinosus* by allowing the plant to have a higher growth performance. Accordingly, the higher growth performance of *A. spinosus* can be attributed to an extremophilic strategy (being more competitive in a stressful environment) rather than either a specialist strategy (being more competitive in a favorable environment) or a generalist strategy (being more competitive in both stressful and favorable environments) [42–44]. Therefore, our results support the second hypothesis.



**Figure 3.** The relative dominance index of *Amaranthus spinosus* in mixed culture under acid deposition with different sulfur–nitrogen ratios. The value of the relative dominance index ranges from 0 to 1, and it means strong growth performance when the value of this index is higher than 0.5, while poor growth performance when the value of this index is less than 0.5. Abbreviations have the same meanings as presented in Figure 1.

Based on the results of this study, there is a great need to slow down, if not stop, the invasion process of *A. spinosus*, especially in mixed culture settings and when exposed to atmospheric pollution, notably acid deposition. Therefore, early warning and preventive control of this invasive plant is essential to maintain ecosystem stability and local biodiversity, especially in wastelands and farmland in East China.

#### 4. Conclusions

In summary, this study is the first to attempt to elucidate the ecological effects of atmospheric pollution, represented by acid deposition with different sulfur–nitrogen ratios, on the functional differences and differences in the growth performance between the invasive and native plant species.

The main findings are as follows: (1) *Amaranthus spinosus* exhibited a strong growth performance over *A. tricolor* in the mixed culture, mainly via the increased leaf photosynthetic capacity. (2) The competitiveness for light acquisition, leaf photosynthetic capacity, and enzymatic defense capacity under stress of *A. spinosus* may be crucial to its growth performance. (3) The lower pH acid deposition exerted a greater negative impact on the growth performance of both *Amaranthus* species than the higher pH acid deposition. (4) Sulfur-rich acid deposition resulted in a greater reduction in the growth performance of both *Amaranthus* species than nitrogen-rich acid deposition. (5) The invasive plant *A. spinosus* was more competitive than the native plant *A. tricolor*, especially when exposed to acid deposition, regardless of the sulfur–nitrogen ratios. Accordingly, acid deposition, regardless of the sulfur–nitrogen ratio, may facilitate the invasion process of *A. spinosus* by enhancing its growth performance.

However, in this study, only six individuals of the same plant species were used per planting pattern to determine the functional differences and differences in the growth performance between *A. spinosus* and *A. tricolor* in mono- and mixed cultures when exposed to acid deposition with different sulfur–nitrogen ratios. In addition, the nitrogen and sulfur contents in the soil and plants were not measured. Thus, future studies will include more plant individuals so as to gain more insights into the differences in the functional traits between invasive and native plants, especially when exposed to acid deposition with different chemical compositions.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/atmos15010029/s1>, Table S1: Four-way ANOVA on the effects of planting pattern, plant species, acid deposition acidity, acid deposition type, and their interactions on the evaluated variances.  $p \leq 0.05$  is presented in bold.

**Author Contributions:** Y.L.: Data curation; Investigation; Methodology; Writing—review and editing; C.L.: Data curation; Investigation; Methodology; Writing—review and editing; S.Z.: Data curation; Investigation; Methodology; Writing—review and editing; Z.X. (Zhelun Xu): Data curation; Investigation; Methodology; Writing—review and editing; J.L.: Data curation; Formal analysis; Writing—review and editing; Z.X. (Zhongyi Xu): Data curation; Formal analysis; Writing—review and editing; M.Z.: Data curation; Formal analysis; Writing—review and editing; C.W.: Conceptualization; Formal analysis; Funding acquisition; Project administration; Supervision; Writing—original draft; D.D.: Funding acquisition; Project administration; Writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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