INVASIVE PLANT ALLIGATOR WEED (*ALTERNANTHERA PHILOXEROIDES* (MART.) GRISEB.) PERFORMS BETTER TO SALINITY, DROUGHT AND ABSCISIC ACID STRESSES THAN NATIVE PLANT SESSILE JOY WEED (*ALTERNANTHERA SESSILIS* (L.))

ABBAS, A.[1] – HUANG, P.[1*] – DU, Y.[2] – HUSSAIN, S.[3] – SHEN, F.[1] – WANG, H.[1] – DU, D.[1*]

[1]*Institute of Environment and Ecology, School of Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China*

[2]*School of Computer Science, Faculty of Engineering, University of Sydney, J12/1 Cleveland St, Darlington NSW 2008, Australia*

[3]*College of Agronomy, Northwest A&F University, Yangling 712100, China*

**Corresponding authors*
e-mail: huangjiehp@ujs.edu.cn; ddl@ujs.edu.cn

(Received 25th Jul 2021; accepted 28th Oct 2021)

Abstract. Invasive plant species have been reported to have advantages over native species in growth- and physiological traits; however, such characteristics have not been discussed under saline, water-scarce conditions. Therefore, the present study was undertaken to investigate the effect of salinity and drought stress and abscisic acid (ABA) application on the morphological and physiological traits of invasive and native weed species. We established three experiments as (i) salinity stress, control with no salt application, 100 and 150 mM NaCl; (ii) drought stress, control-no drought, 75 and 100 gL^{-1} PEG-6000; and (iii) ABA application, control-no application, 25 and 50 ulL^{-1}. Two weed species, the invasive *Alternanthera philoxeroides* and native *Alternanthera sessilis*, were used in all experiments. The study was laid out in a completely randomized design (CRD) with factorial arrangements and twelve replications. Results revealed that both invasive *A. philoxeroides* and native *A. sessilis* species survived under high salt and drought stress conditions. *A. philoxeroides* species generally showed higher morphological and physiological growth under high salt and drought levels, showing higher tolerance to stress conditions than *A. sessilis*. Moreover, the morphological and physiological traits of *A. philoxeroides* were elevated more under ABA application. Our results showed higher values of morpho-physiological traits might partly explain the success of *A. philoxeroides* under saline and drought conditions.
Keywords: *invaders, abiotic stresses, growth, water deficit stress, polyethylene glycol, physiological attributes, comparative analysis*

Introduction

Invasive weeds are among the major problems for crop production, and also exerts a harmful impact on the environment (Pyšek and Richardson, 2008; Balachandar et al., 2021). The typical approach used to study these plants is to compare them with their native counterparts (Kettenring and Adams, 2011). However, only limited studies have discussed the performance of invasive and native species under different environmental conditions (Yu and He, 2021). It is commonly known that invasive species can perform better under abiotic stress stimuli, in terms of higher growth rate, effective resource use efficiency, and reproducibility capacity, compared with their native species (Funk, 2013). In a comparative study of native and invasive species, Godoy et al. (2011)

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2002_11731187

reported that invasive species had performed better even under limited resource availabilities than their native ones. Also, in a meta-analytic study, invasive weeds have been reported as more dominant in morphological and physiological traits than native species (Palacio-López and Gianoli, 2011). However, in some studies, authors have reported higher growth rate and resource use efficiencies in terms of greater instantaneous photosynthetic energy-use efficiency and photosynthetic nitrogen-use efficiency in native species than invasive plants (Heberling and Fridley, 2013). Among invasive weeds, *Alternanthera philoxeroides* is an amphibious stoloniferous perennial herb native to South America, and firstly was introduced to China and Japan as a forage crop (Myanmar et al., 2016). It is characterized as a higher growth rate and vegetative reproduction than their corresponding native species (Yang et al., 2019). Also, new plants are produced through the splitting from roots and stems (Amsellem et al., 2000). Now a days, it is found across the globe, both in aquatic and terrestrial environments. *A. philoxeroides* had dominant characteristics and diversified habits in term of better plasticity to cope with different abiotic stresses (Chen et al., 2013). Additionally, it can re-grow aggressively under extreme conditions and has dominant biological control through their morphological traits (Zuo et al., 2012). *A. philoxeroides* have the ability to grow rapidly under different abiotic stresses, including long submerged conditions (Fan et al., 2015).

Furthermore, *Alternanthera sessilis* is an amphibious dicotyledon, as invasive weed can grow abundantly in disturbed areas and in moist and dry soils (Abbasi et al., 2019). It is a pioneer species typically growing on marginal lands, ranging from poor sandy/alkaline soils to loam soils, and it can be found in invading floodplain wetlands, margins of rivers, streams, canals, and damp forest. It is regarded as fast-growing species in dry regions as well as in seasonally-waterlogged areas and is defined as a weed in fields with different crops (Holm et al., 1997; Gupta, 2014). Consequently, this species has been reported as invasive in different countries and as a noxious weed in the United States (USDA-NRCS, 2014). It becomes particularly harmful for paddy and other extensive irrigated crops due to its allelopathic effects (Kumar et al., 2020). Both *A. sessilis* and *A. philoxeroides* are dominant in nature and grow well even under abiotic stress conditions. While adapting to different environmental stresses, these species pass through various changes at morphological, physiological, and molecular levels (Mallick et al., 2019). By reducing the leaf water potential and slow down the growth and development, these species adapt well under stress conditions (Parkash and Singh, 2020). Drought is a significant abiotic stress, can influence the various physiological and biochemical functions, including reduced photosynthesis and chlorophyll synthesis (Dong et al., 2016; Wang et al., 2018). In addition to drought stress, high salt concentrations in rhizosphere also restrict the plant growth and development (Vurukonda et al., 2016); however, the inhibitory effects of salt stress vary with salt types, plant growth stage, and environmental conditions (Shahverdi et al., 2018). Variable growth responses of different weed species have been documented under drought stress (Webster and Grey, 2008; Chauhan, 2013). Drought stress markedly reduced the photosynthetic rates, mainly through the closure of stomata, reduced mesophyll conductance, and supply of carbon dioxide (CO_2) (Sagardoy et al., 2010).

Moreover, it is commonly known that abscisic acid (ABA) is a crucial regulator during plant responses to stresses, and torrent weeds can accumulate ABA faster than that of sanative weeds (Radhakrishnan et al., 2016). Abscisic acid also reported to play

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an essential role in maintaining the plant growth under different stress conditions (Vishal and Kumar, 2018). As discussed above, in recent years, many studies have conducted on the comparative performance of *A. sessile* and *A. philoxeroides*. However, little is known regarding the comparative performance of these species under abiotic stress conditions. Therefore, for this work, it was hypothesized that *A. philoxeroides* showed better performance under drought and salt stress than *A. sessile*. For this study, our specific objectives were (a) to investigate the performance, in terms of morphological and physiological traits, of native and invasive weeds under drought and salt stresses, (b) and to evaluate the effectiveness of these weed species to exogenous ABA application.

Materials and methods

Experimentation and treatments implementation

The experiment was performed under greenhouse conditions at Jiangsu University, Jiangsu (32.20°N, 119.45°E), China. Ramets of *A. sessilis* and *A. philoxeroides* were collected outside of the greenhouse, where they were grown for experimental studies. To culture the plant materials, the rooted seedlings were cut into ramets of equal lengths. Ramets were prepared in seedling trays with sand as a culture medium. These trays were placed in a greenhouse, where the temperature of 25 ± 5 °C during the day, 18 ± 2 °C during the night, and 70% relative humidity were maintained throughout the experimental period. All these seedlings were subjected to normal daily watering. When these ramets had two fully expanded leaves, they were sampled and re-planted into the plastic pots (having height of 10 cm, outer- and inner diameter of 13 and 6 cm, respectively) for salinity and ABA experiments and to hydroponic culture for drought experiment. After one week of seedling transfer, the treatments were imposed. In experiments I and III (salinity and ABA application), there were total of 72 plastic pots for each experiment and filled with well-sieved sandy soil. The physical and chemical properties of the soil used for pot filling are given in *Table 1*. In experiment II, for imposition of drought stress, plants of invasive and native species with two fully expanded leaves were cultivated in hydroponic culture with Hoagland nutrient solution (Hoagland and Arnon, 1950). After seven days of transplanting, drought treatments were imposed as control-no drought, 75 g L^{-1} PEG 6000, and 100 g L^{-1} PEG 6000. The nutrient solution was continuously aerated throughout the experimentation. In experiment I, salinity treatments included on: control-no salt application, 100 mM NaCl and 150 mM NaCl. In experiment III, abscisic acid was applied as control, (no ABA application), 25 ul L^{-1} and 50 ul L^{-1} (*Table 2*). The study was laid out in a completely randomized design (CRD) with factorial arrangements, and there were total twelve replications.

Table 1. *Physical and chemical characteristics of sandy soil used for pot filling*

Soil parameter	Sandy soil
pH	6.60
Organic matter %	0.34
Total nutrient %	0.98
Water content %	15
Electrical conductivity Ds m^{-1}	1.2

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Table 2. *Treatment plan for different experiments*

Experiments	**Treatments**		
	T1	**T2**	**T3**
Experiment-I (salt stress)	Control	100 mM NaCl	150 mM NaCl
Experiment-II (drought stress)	Control	75 g L^{-1} PEG-6000	100 g L^{-1} PEG-6000
Experiment-III (abscisic acid application)	Control	25 ul L^{-1}	50 ul L^{-1}

Data recording

Morphological and chlorophyll data

Fifteen days after treatments application, plants were harvested for the measurement of growth and physiological traits. From each treatment, six plants were selected for the measurement of growth and physiological parameters. Plant height was measured using a ruler and fresh and dry weights of seedlings by using a weighing balance. Each plant was separated into roots and leaves, dried at 60 °C for 48 h, and weighed. A plant chlorophyll meter (Oakoch OK-Y104, China) was used to measure the stomatal conductance, net photosynthesis rate, water use efficiency, and intercellular CO_2. Young leaves were preferably selected for evaluating the photosynthetic attributes. All data were recorded during full sunshine at 9:30–11:30 a.m. The following settings were noted on chlorophyll meter during data collection: photosynthetic active radiation (PAR) of 800 μmol m^{-2} s^{-1}, the temperature of 28 °C and CO_2 concentration of 500 μmol mol^{-1}.

Statistical analysis

Data analysis was performed statistically with SPSS 17 software (SPSS, IL, USA). Before further analysis, assumptions of parametric statistics were tested to verify the normality and homogeneity of variance using the Shapiro–Wilk normality test and Levene’s test. A one-way analysis of variance (ANOVA) technique was applied to examine the impact of different levels of salinity, drought, and abscisic acid on the growth and physiological traits of *A. sessile* and *A. philoxeroides*. The least significant difference test at 5% probability level was applied to determine the differences between means (n = 12).

Results

Experiment 1: impact of salt stress on the performance of native and invasive weed species

Growth measurements

The growth traits (fresh and dry root weight, fresh and dry leaf weight, plant height, and dry weight biomass) of both *A. philoxeroides* and *A. sessilis* remained unaffected by salt stress treatments (*Table 3*; *Fig. 1*). Nonetheless, all growth measures differed significantly for both *A. philoxeroides* and *A. sessilis* species (*Fig. 1*). Regardless of salt treatments, *A. philoxeroides* recorded an increase in fresh root weight by 45.91%, dry root weight by 172.63%, fresh leaf weight by 50.78%, dry leaf weight by 66.40%, plant height by 46.56%, and dry weight biomass by 21.75%, respectively, compared to *A. sessilis* on

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average. Moreover, there was a non-significant salt treatment × species interaction for all growth traits except for plant height and total dry weight biomass (*Table 3*; *Fig. 1*).

Physiological attributes

Salt stress did not have same effect on the physiological attributes of both species. For instance, the intracellular CO_2 and net photosynthesis rate in both *A. philoxeroides* and *A. sessilis* species did not differ under salt stress (*Fig. 3*). However, salt treatments significantly affected the stomatal conductance and water use efficiency in both species (*Table 3*; *Fig. 2*). In general, there was a significant difference for all physiological traits, including stomatal conductance, net photosynthesis rate, water use efficiency and intercellular CO_2 of both species. Compared to *A. sessilis*, an increase in intracellular CO_2 by 8.89%, stomatal conductance by 20.35%, and water use efficiency by 52.46% were recorded for *A. philoxeroides* on average. Moreover, there was a non-significant salt treatment × species interaction for all physiological traits (*Table 3*).

Experiment 2: Impact of drought stress on the performance of native and invasive weed species

Growth measurements

In this study, drought stress did not influence all growth measures of both *A. philoxeroides* and *A. sessilis* (*Table 3*; *Fig. 3*). Among native and invasive species, there was a significant difference for all growth traits. Regardless of drought treatments, *A. philoxeroides* reported an increase in fresh root weight by 71.66%, dry root weight by 139.09%, fresh leaf weight by 27.47%, dry leaf weight by 57.72%, plant height by 19.45%, and dry weight biomass by 21.83% compared to *A. sessilis* on average. Moreover, the only significant drought treatment × species interaction was for plant height (*Table 3*).

Table 3. *Influence of salt and drought stresses and ABA application on morphological and physiological traits of A. sessilis and A. philoxeroides*

Variables	Salt stress			Drought stress			Abscisic acid application		
	Treatment	Species	T × S	Treatment	Species	T × S	Treatment	Species	T × S
Morphological traits									
FRW	2.11^{ns}	44.65**	0.75^{ns}	0.43^{ns}	199.45**	0.03^{ns}	0.08^{ns}	84.30**	1.51^{ns}
DRW	2.91^{ns}	684.99**	1.55^{ns}	0.58^{ns}	446.44**	2.46^{ns}	1.96^{ns}	463.00**	1.14^{ns}
FLW	0.83^{ns}	131.32**	0.00^{ns}	1.64^{ns}	39.30**	0.05^{ns}	57.58^{ns}	1.76**	0.85^{ns}
DLW	0.24^{ns}	54.58**	0.21^{ns}	0.31^{ns}	63.45**	1.00^{ns}	0.13^{ns}	103.29**	0.31^{ns}
PH	6.43^{ns}	216.34**	0.44**	1.62^{ns}	29.20**	1.10*	0.43^{ns}	50.88**	0.11^{ns}
DWB	0.44^{ns}	24.98**	1.15*	0.68^{ns}	38.17**	0.64^{ns}	1.40^{ns}	20.78**	0.29^{ns}
Physiological traits									
iCO_2	0.81^{ns}	6.46*	0.34^{ns}	0.94^{ns}	0.60^{ns}	0.14^{ns}	0.11^{ns}	4.72*	0.11^{ns}
SC	5.81**	9.20*	0.61^{ns}	5.08*	7.34**	0.78^{ns}	3.88*	41.13**	0.12^{ns}
NPR	1.44^{ns}	21.21**	0.68^{ns}	2.49^{ns}	33.91**	0.32^{ns}	4.43*	12.24*	1.03^{ns}
WUE	6.30**	61.42**	0.30^{ns}	3.05^{ns}	4.31^{ns}	0.91^{ns}	11.70**	10.06**	3.17^{ns}

FRW, fresh root weight; DRW, dry root weight; FLW; fresh leaf weight; DLW, Dry leaf weight; PH, plant height; DWM, dry weight biomass; iCO_2 intracellular CO_2; SC, stomatal conductance; NPR, net photosynthesis rate; WUE, water use efficiency

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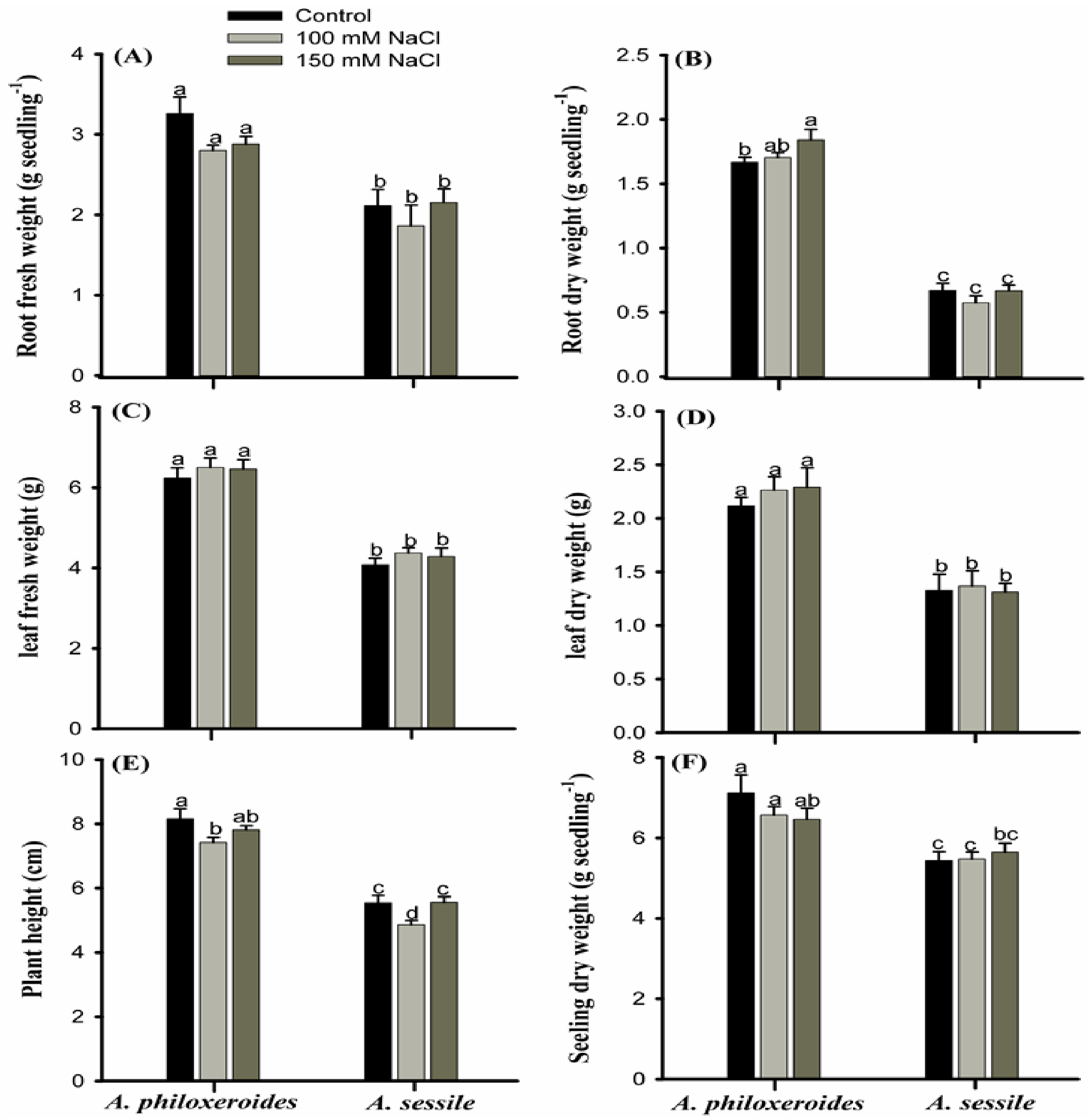

Figure 1. *Fresh root weight (A), dry root weight (B), fresh leaves weight (C), dry leaf weight (D), plant height (E), and dry weight biomass (F) of A. philoxeroides and native A. sessilis plants exposed to different levels of salt stress. The data are presented as the means ± S.E., n = 12. Different letters above bars indicate significant differences among treatments at (P < 0.05)*

Physiological attributes

Physiological measures in both species did not differ significantly between drought treatments, except for stomatal conductance of both species (*Fig. 4*). However, there was a significant difference in all physiological traits between *A. philoxeroides* and *A. sessilis*, except for intracellular CO_2 and water use efficiency (*Fig. 4*). The stomatal conductance and net photosynthesis rate of *A. philoxeroides* were increased by 14.74 and 61.51%, respectively, compared to *A. sessilis* on average (*Fig. 4*). In addition, there was a non-significant drought treatment × species interaction for all physiological traits (*Table 3*).

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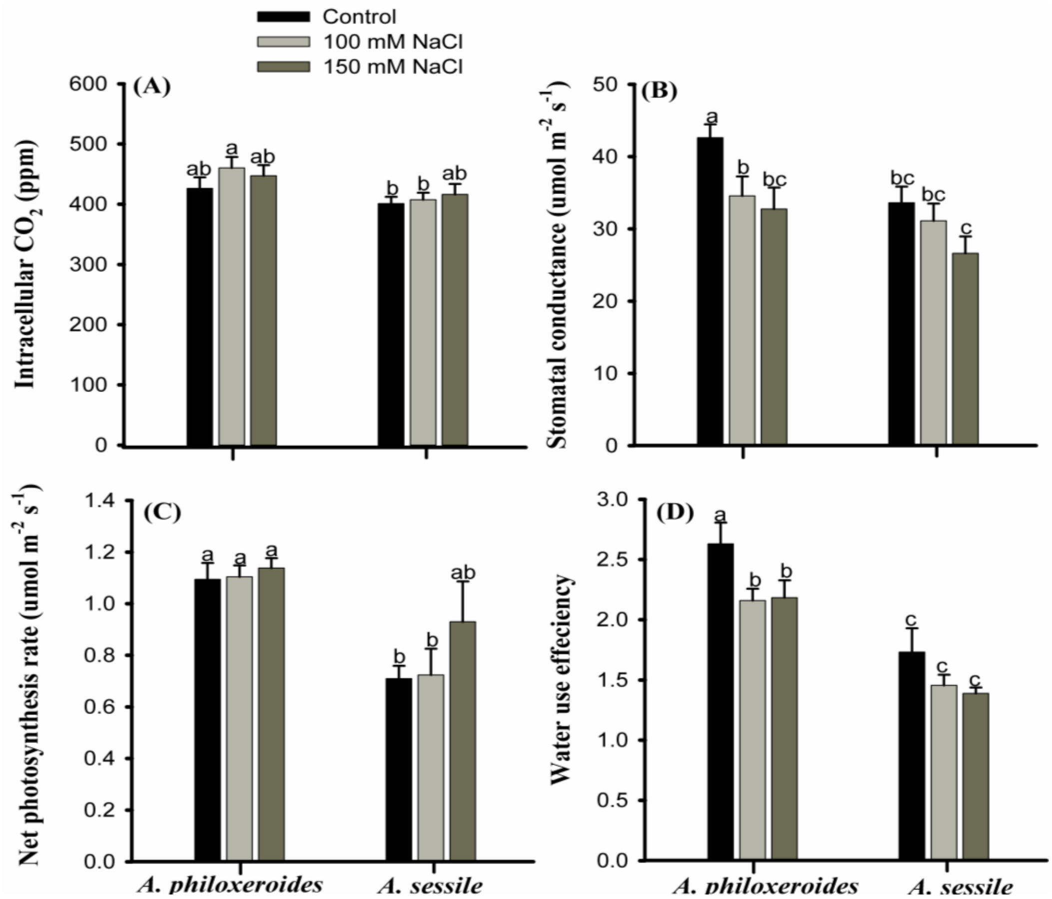

Figure 2. *Intracellular CO_2 (A), stomatal conductance (B), net photosynthesis rate (C), and water use efficiency (D) in A. philoxeroides and native A. sessilis plants exposed to salt treatments. The data are presented as the means ± SE, n = 12. Different letters above bars indicate significant differences among treatments at (P < 0.05)*

Experiment III: Comparative performance of native and invasive weed species under ABA application

Growth measurements

Abscisic acid (ABA) application non-significantly affected the growth measures in both species (*Fig. 5*). Nonetheless, all growth measures were differed significantly for both *A. philoxeroides* and *A. sessilis* species. Overall, for the individual effect of species, *A. philoxeroides* showed greater values of growth measures than *A. sessilis.* An increase in fresh root weight by 90.74%, dry root weight by 145.96%, fresh leaf weight by 48.35%, dry leaf weight by 56.10%, plant height by 26.12%, and dry weight biomass by 19.78% was noted for *A. philoxeroides*, as compared to *A. sessilis* on average. Moreover, there was a non-significant ABA treatment × species interaction for all growth parameters (*Table 3*).

Physiological attributes

Data regarding the physiological activities (i.e., intracellular CO_2, stomatal conductance, net photosynthesis rate and water use efficiency) of both *A. philoxeroides* and *A. sessilis* species under ABA application are presented in (*Fig. 6*). ABA

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application significantly affected both species' stomatal conductance, net photosynthesis rate, and water use efficiency. However, there was a non-significant difference for intracellular CO_2 under ABA application. In general, there was a significant difference for all these traits of both *A. philoxeroides* and *A. sessilis* species (*Fig. 6*). Compared to *A. sessilis*, an increase in intracellular CO_2 by 8.40%, stomatal conductance by 37.66%, net photosynthesis rate by 39.54%, and water use efficiency by 31.55% was recorded for *A. philoxeroides* on average. Moreover, there was a non-significant ABA treatment × species interaction for all physiological traits (*Table 3*).

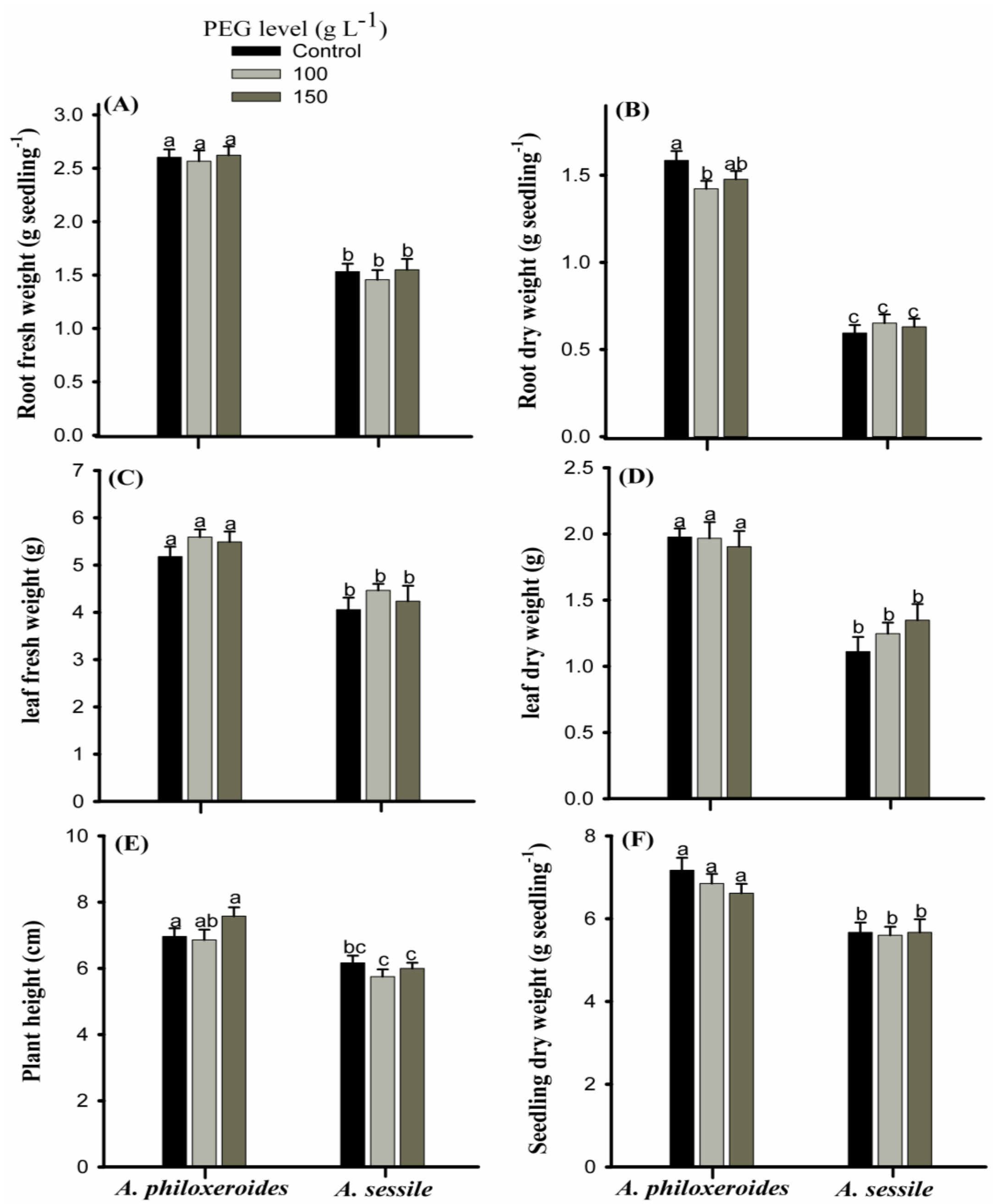

Figure 3. *Fresh root weight (A), dry root weight (B), fresh leaves weight (C), dry leaves weight (D), plant height (E), and dry weight biomass (F) of A. philoxeroides and native A. sessilis plants exposed to drought stress. The data are presented as the means ± SE, n = 12. Different letters above bars indicate significant differences among treatments at (P < 0.05)*

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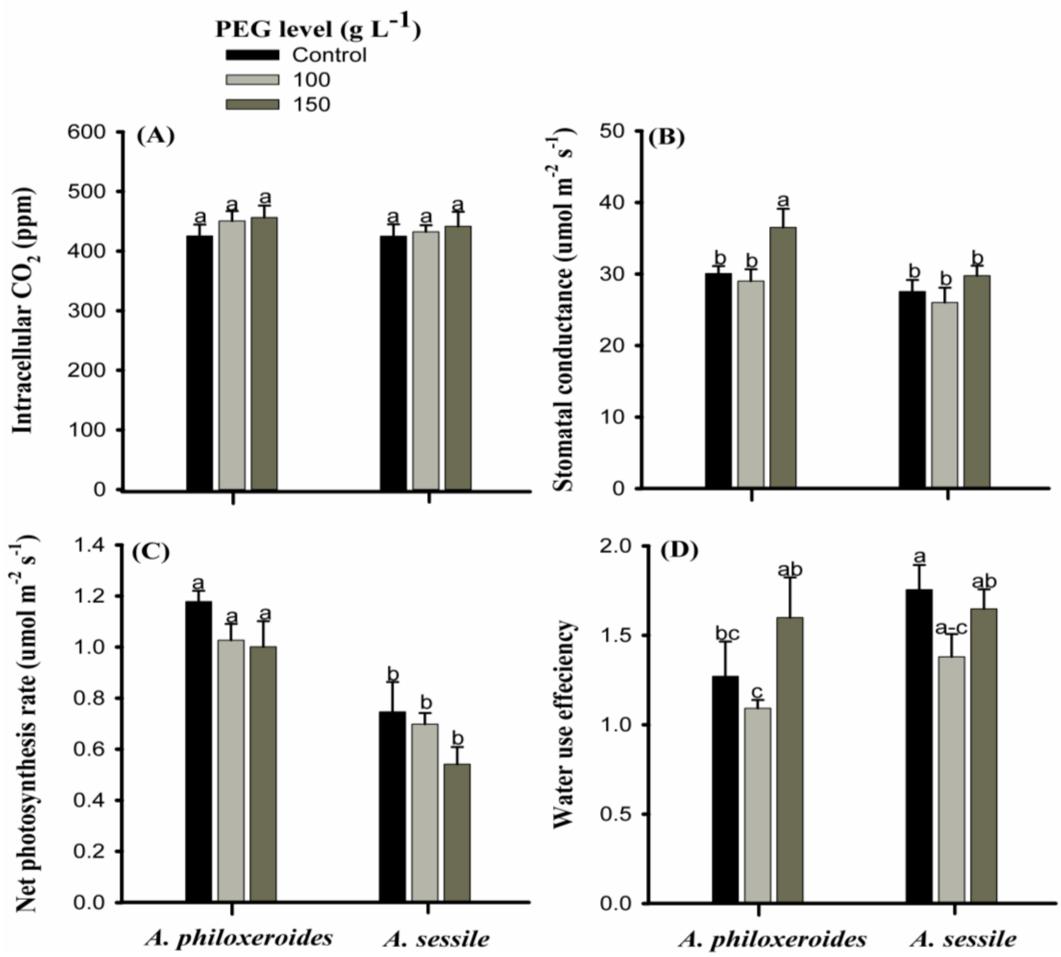

Figure 4. *Intracellular CO_2 (A), stomatal conductance (B), net photosynthesis rate (C), and water use efficiency (D) in A. philoxeroides and native A. sessilis plants exposed to drought stress. The data are presented as the means ± SE, n = 12. Different letters above bars indicate significant differences among treatments at ($P < 0.05$)*

Discussion

Among abiotic stresses, salinity and drought are the major limiting factors for crop plant growth and productivity (Fita et al., 2015). Although major studies discuss the impact of abiotic stresses on field-grown crops (James et al., 2018), only a few studies have examined the comparative performance of native and invasive weed species under environmental cues (Gioria and Pyšek, 2017). In this experiment, salinity and drought stress did not affect the growth of both invasive *A. philoxeroides* and native *A. sessilis* species, indicating their tolerance abilities to salinity and drought stress (*Figs. 1, 3*). These findings are inconsistent with the results of (Chen et al., 2013), who reported that stress (waterlogged) conditions decreased the growth of both native and invasive species. Similarly, according to (Madawala et al., 2014), high soil salinity influences both native and invasive species.

Performance of invasive and native species under salt stress

Invasive *A. philoxeroides* and native *A. sessilis* species differed in growth and physiological traits under a salt environment (*Fig. 1-2*). In general, *A. philoxeroides*

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recorded significantly more values of growth traits than *A. sessilis* (*Fig. 1*). In agreement with these findings, Monaco et al. (2016) reported that invasive *Bromus diandrus* accumulated significantly higher total biomass than the native *Bromus carinatus* under salt stress. Invasive species grow under salt stress mainly due to their higher growth rate. Similar findings were also reported for waterlogging stress (Chen et al., 2013). The authors reported that *A. philoxeroides*, an invasive species, showed more reduction in growth traits under waterlogged conditions than *A. sessilis*. Compared to non-invasive species, higher growth rates of invasive species have been well documented in previous studies (Van Kleunen et al., 2010). The physiological traits under salinity also differed between invasive and native species (*Fig. 1*). Compared to *A. sessilis*, an increase in intracellular CO_2, stomatal conductance, and water use efficiency was recorded for *A. philoxeroides*. Our results consisted of previous studies, which showed that *A. philoxeroides* showed greater physiological traits under heat and drought stress (Geng et al., 2006; Sun et al., 2010). Higher root to shoot ratio and chlorophyll concentrations of *A. philoxeroides* under stress conditions might reduce the respiratory losses and improve the light interception, availability of oxygen, and carbohydrate status of plants (Luo et al., 2011; Zhang et al., 2020).

On the other hand, in *A. philoxeroides*, leaves necrosis under stress conditions (Chen et al., 2013) might also reduce respiratory failure (Colmer and Voesenek, 2009). It is generally believed that by producing more carbon-rich compounds, the invaders (invasive) avoid excessive irradiance (Godoy et al., 2011) and disposes of enough carbon to reduce the carbon trade-off between growth and tissue protection (Villar et al., 2006), thereby reducing the risk of photo-inhibition causing damage to chlorophyll, which in turn can increase the carbon gain and crop growth (Naciri et al., 2021). Compared to *A. sessilis*, a less decline in growth traits and higher values of physiological parameters under salinity might contribute to higher tolerance of *A. philoxeroides* (*Figs. 1-2*). A relatively more substantial decline in growth traits of *A. sessilis* suggesting more sensitivity to environmental stresses (Javed et al., 2019).

Performance of invasive and native species under drought stress

Both *A. philoxeroides* and *A. sessilis* did not differ regarding growth traits (dry root and plant biomass, and fresh leaf weight) under drought stress (*Fig. 3*). However, *A. philoxeroides* had increased the dry root weight, fresh leaf weight, and dry weight biomass compared to *A. sessilis* (*Fig. 3 A, C*). These findings are consistent with previous reports that invasive species showed higher growth rate than native species (Van Kleunen et al., 2010). However, these results are inconsistent with earlier findings of Molina-Montenegro et al. (2011), where the authors have reported lower biomass and leaf size in invasive species than in native type during water scares conditions. In this study, under drought stress, there was a significant difference in physiological traits for both species (*Fig. 4*). Stomatal conductance, net photosynthesis rate, and water use efficiency were increased significantly in *A. sessilis* than in *A. philoxeroides*. These findings do not match previous studies suggesting that invasive showed higher values of physiological traits (photosynthesis and transpiration rates, and water use efficiency) than native species (Van Kleunen et al., 2010; Godoy et al., 2011). Similarly, in contrast to our findings, Chen et al. (2013) have reported that invasive *A. philoxeroides* showed the ability to maintain the photosynthetic capacity even under stress conditions.

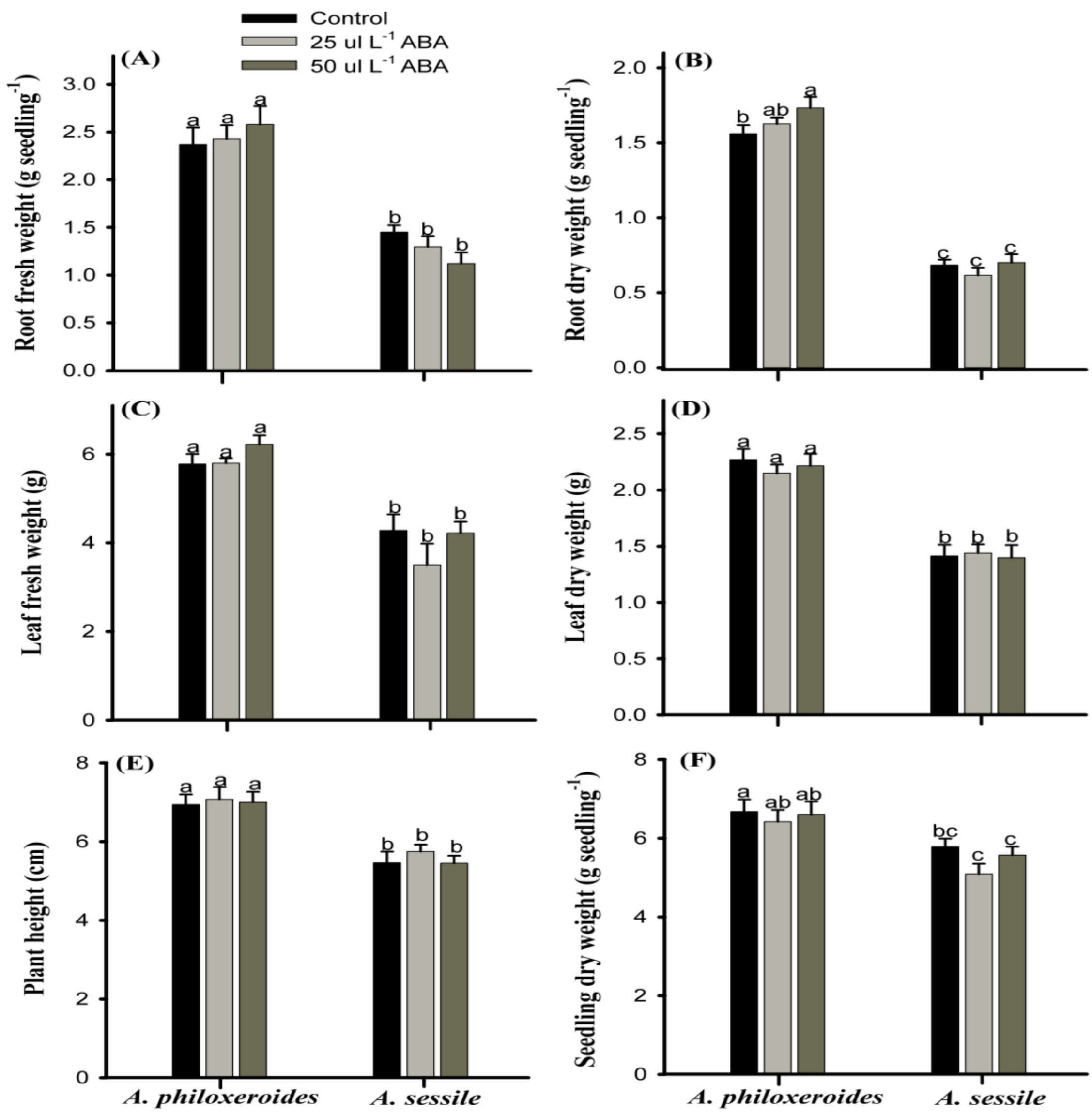

Figure 5. *Influence of abscisic acid (ABA) application on Fresh root weight (A), dry root weight (B), fresh leaves weight (C), dry leaves weight (D), plant height (E), and dry weight biomass (F) of A. philoxeroides and native A. sessilis plants. The data are presented as the means ± SE, n = 12. Different letters above bars indicate significant differences among treatments at (P < 0.05)*

Response of invasive and native species to abscisic application

For the first time, our results have reported the performance of invasive and native species under ABA application. In this study, *A. philoxeroides* recorded significantly higher values of growth measures and physiological traits than *A. sessilis* under ABA application (*Fig. 6*). These findings are inconsistent with previously published reports that suggest that seedling growth in most of the invasive species significantly inhibited under ABA application (Liu et al., 2015). In *A. philoxeroides*, higher values of growth traits may be due to improved water relations of the plants under ABA application. Abscisic acid acts as an endogenous messenger in regulating plant-water status (Rai et al., 2011). The enhanced plant growth under ABA application has been

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well documented in various studies (Wei et al., 2015, 2017). In addition, ABA application may also result in the closure of stomata and reduced transpirational water loss (*Fig. 6*).

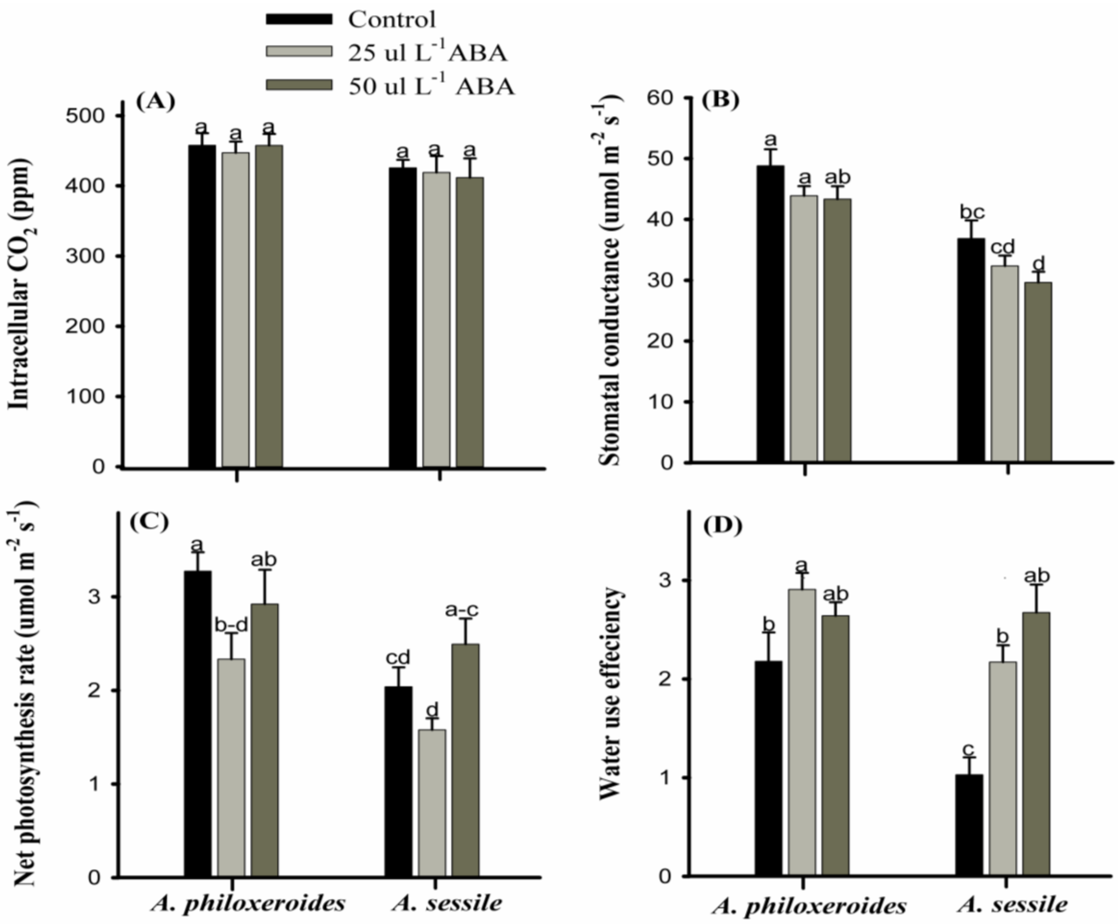

Figure 6. *Influence of abscisic acid (ABA) application on intracellular CO_2 (A), stomatal conductance (B), net photosynthesis rate (C), and water use efficiency (D) in A. philoxeroides and native A. sessilis weeds. The data are presented as the means ± SE, n = 12. Different letters above bars indicate significant differences among treatments at ($P < 0.05$)*

Conclusion

In sum, the results of this study showed that both invasive *A. philoxeroides* and native *Alternanthera sessilis* showed great tolerance to salt and drought stress. In general, under stress conditions, two species differed in growth and physiological traits: *A. philoxeroides* displayed higher values of morphological and physiological characteristics. In addition, under ABA application, *A. philoxeroides* showed less sensitivity as compared to *A. sessilis*. Higher tolerance of salt and drought stress may partly explain the ability of *A. philoxeroides* to invade saline and water-scarce areas. We predict that *A. philoxeroides,* which is dominant invasive species, might have the potential to become a serious problem in saline soils, including coastal areas, and in dry areas in the future. More attention should focus on monitoring the occurrence of *A. philoxeroides* on saline soils and in dry areas, timely prevention should be implemented to control new invaders.

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Funding. This work was supported by the National Natural Science Foundation of China (32071521, 31200316), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), the Jiangsu Collaborative Innovation Center of Technology and Material of Water Treatment, Study Abroad Scholarship of Jiangsu University, Senior Talent Fund of Jiangsu University (11JDG150).

Conflict of interests. The authors declare no conflict of interests.

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