*Pol. J. Environ. Stud. Vol. 31, No. 4 (2022), 2987-2995*
DOI: *10.15244/pjoes/142474* ONLINE PUBLICATION DATE: 2022-04-26

*Original Research*

# Mild Evidence for Local Adaptation of *Solidago canadensis* under Different Salinity, Drought, and Abscisic Acid Conditions

**Adeel Abbas[1], Ping Huang[1*], Sadam Hussain[2], Fangyuan Shen[1], Hao Wang[1], Daolin Du[1**]**

[1]Institute of Environment and Ecology, School of Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China
[2]College of Agronomy, Northwest A&F University, Yangling, 712100, China

*Received: 16 July 2021*
*Accepted: 21 September 2021*

## Abstract

*Solidago canadensis* is an invasive weed that grows successfully under adverse environmental conditions and shows a high capability to various habits. To evaluate the role of local adaptation in the invasion of *S. canadensis* into heterogeneous environments, the morphological and physiological traits of *S. canadensis* plants were studied under salt (control, 100 and 150 mM NaCl), drought stress conditions (control, 75 and 100 g $L^{-1}$ PEG-6000) and abscisic acid (ABA) (0, 25, and 50 ul $L^{-1}$) application. Salt treatments significantly reduced the plant height, shoot dry weight (SDW), water use efficiency (WUE), intracellular $CO_2$, and net photosynthetic rate (NPR) by 8.17, 28.75, 21.65, 20.71 and 35.44%, respectively than control plants. Among salt treatments, maximum reduction was found under 150 mM NaCl followed by 100 mM NaCl and control treatment. Salt treatments demonstrated a nonsignificant effect on leaf fresh and dry weight, root length and stomatal conductance. Similarly, drought stress significantly reduced the leaf fresh weight, leaf dry weight, plant height, stomatal conductance, and NPR with maximum reduction under severe drought condition (100 g $L^{-1}$ PEG-6000), where the values were 31.01, 30.39, 35.09, 49.19 and 46.93% lower respectively than control plants. In this study, ABA application had not significantly influenced the morpho-physiological traits of *S. canadensis*. Reduced plant height, SDW and NPR under both stresses and reduced WUE and intracellular $CO_2$ under salt stress suggest some degree of phenotypic plasticity under these stress conditions.

**Keywords**: local adaptation, invasive weeds, salinity, drought, physiological traits, abscisic acid

---

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

## Introduction

Invasive weeds species are considered as a serious threat and danger to biodiversity in habitat destruction and a primary hotspot in environment and ecology studies [1]. Introducing alien and new plants into a novel region encounters biotic and abiotic stresses that may ascertain their invasion process [2]. It is well reported and documented in previous studies that invasive weeds have strong adaptation ability to different environmental fluctuations as compared with their natives' species [3, 4]; still, there is no adequate study which provides any evidence regarding the equal ability of native and invasive weeds against different biotic and abiotic stresses [5]. Moreover, it remains unclear how invasive weeds adapt quickly under variable environmental conditions [6, 7].

Plants are sessile in nature and show friction in their life cycle. They are subjected to perform better and have strong selection and adaptation abilities against local environmental conditions [8]; these local adaptations promote extensive dissemination and productive occupation of different habitats [9]. Someway geographical distribution and variation lead to different adaptational processes to the local environment and play a vital role in developing functional traits against various abiotic stresses [10, 11]. Overall, local adaptation is considered as well verified invasive weed mechanism to enhance invasiveness [12], leading plants to adapt against different biotic and abiotic stresses [12]. In other words, phenotypic can produce phenotypes against different environmental variation responses [14] and contribute to the success of invasive plants by permitting fitness across the habitats range and playing a vital role in the successful formation under different and new environmental conditions [13]. A fundamental and prominent issue in invasive plant dominancy is to determine the importance of phenotypic plasticity and local adaptation in invasive plants' success to different environmental fluctuations throughout the distribution process [14]. However, ambiguous conclusions indicate the importance of this factor dependence of different plant species, including their different physiological and molecular characteristics [15]. That is why more attention and contribution are needed to invasive plants to explore their invasion process and success against different abiotic stresses [16].

Among abiotic stress, salinity and drought stress determine how colonization, and high salinity can affect plant growth and the development process [17]. It is reported in many studies that salinity causes many disorders in plants at morpho-physiological, biochemical, and molecular levels. It inhibits plant growth by reducing water uptake, ionic imbalance by increasing toxicity level [18-20]. However, salinity effects on plant growth depending on salt types and concentrations [21]. High salinity effects and decreases photosynthesis rate and other morpho-physiological traits (plant height, number of leaves, root length and dry weight biomass, etc.) [22]. In contrast, low salinity accelerates plant growth and development [23]. In salt tolerant plant species, local adaptations contribute strongly and play a vital role in the invasion process and success [24,25]. Salinity stresses enhance *Spartina alterniflora* (native) replacement by *Phragmites australis* (invasive) [26]; on the other hand, salinity stress decreases *Salicornia subterminalis* replacement by *Polypogon monspeliensis* invasion [27]. To understand the response against salinity stress, plants show the potential for colonization, physiological changes, and different management strategies provides references in invasion studies [28]. Monitoring changes in chlorophyll fluorescence and photosynthesis rate under drought stress provides a signal to the distribution of *Chromolaena odorata.* Plants' responses to salinity and drought are varied for morphological and physiological traits [29]. Moreover, it is commonly known that abscisic acid (ABA) is a crucial regulator during a plant's response to stresses, and tolerant weeds accumulate ABA faster than sensitive ones [30]. ABA also reported to play an essential role in maintaining plant growth under different stress conditions [31].

*Solidago canadensis* L., a forb belonging to the *Asteraceae* family, can form aboveground clonal shoots from persistent belowground rhizomes [32]. Initially, *S. canadensis* was introduced as ornamental plant, but later it was changed into wild and become abundant across China [33]. Based on growth chamber and greenhouse experiments, *S. canadensis* evolved rapidly in different regions and was reported have the ability to perform better against various abiotic stresses [34]. However, it is still reported that individual plasticity without local adaptation plays an essential role in *S. canadensis* response against different abiotic stresses [35]. *S. canadensis* also showed salinity tolerance and invaded sandy loam soil significantly in the coastal areas of East China [36]. Concerning different abiotic stresses (salinity and drought) and ABA different concentration levels, we assumed that local adaptation might play a critical role in the invasion process against different salinity and droughty conditions. We conducted a greenhouse experiment with replicate cuttings of *S. canadensis* with the following questions: (1) are drought and salinity stress affect the performance of *S. canadensis*? (2) Do *S. canadensis* perform better under high levels of salt and drought than low levels? (3) How does *S. canadensis* react against ABA application?

## Experimentation and Treatments Implementation

The experiment was performed under greenhouse conditions at Jiangsu University, Jiangsu (32.20°N, 119.45°E), China, where the temperature of 25±5ºC during the day, 18±2ºC during the night, and 70% relative humidity were maintained throughout the experimental period. In the winter of 2019, *S. canadensis* seeds were collected from the roadside of Zhenjiang, Jiangsu province, China. No specific permissions were required for these locations. Initially, *S. canadensis* seeds were sown in seedling tray with sand, and 14 days old seedlings were used for further experiments. For salinity stress and ABA application, seedlings were transferred into pots (with 10 cm height, outer- and inner diameter of 13 and 6 cm, respectively) and to hydroponic culture for drought experiment. When these seedlings were fully established in pots and hydroponic culture, salinity, drought, and ABA application started. For salinity stress and ABA experiments, a total of 72 pots for each experiment were filled with well-sieved sandy soil. The physical and chemical properties of the soil used for pot filling are given in Table 1. For the drought experiment, seedlings with fully expanded leaves were cultivated in hydroponic culture with Hoagland nutrient solution [37]. After seven days of transplanting, drought treatments were imposed as control (no drought), 75 and 100 g $L^{-1}$ PEG (6000). The nutrient solution was continuously aerated throughout the experimentation. In the salinity experiment, the treatments were included on control (no-salt application), 100 and 150 mM NaCl. Abscisic acid treatments were included on a control (no-ABA application), 25 ul $L^{-1}$ and 50 ul $L^{-1}$. The study was laid out in a completely randomized design (CRD) with factorial arrangements, and there were a total of twelve replications.

## Data Recording

### Morphological and Chlorophyll Data

From each treatment, six plants were selected for the measurements of growth and physiological parameters. Plant height (PH) was measured using a ruler. The fresh and dry weights of plant above ground (stem and leaf) and below ground (root) biomass of each individual was measured separately. For dry weight, samples were oven dried at 72ºC for 48 h and weighing the samples by using a weighing balance. A portable 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 the chlorophyll meter during data collection: active photosynthetic radiation (PAR) of 800 µmol $m^{-2}$ $s^{-1}$ (i.e. at light saturation), leaf temperature of 28ºC, and $CO_2$ concentration of 500 µmol $mol^{-1}$.

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 |

### 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. One-way analysis of variance (ANOVA) technique with t-test (at $P<0.05$) was used to examine the impact of different salinity levels, drought, and abscisic acid on the growth and physiological traits of *S. canadensis*.

## Results

### Effect of Salinity on Growth and Physiological Traits

Salt treatments had a significant effect on plant height (Fig. 1d), $p = 0.01$), seedling dry weight (Fig. 1e), $p = 0.001$), water use efficiency (Fig. 1f), $p = 0.01$), intracellular $CO_2$ (Fig. 1h), $p = 0.001$), and net photosynthetic rate (Fig. 1i), $p = 0.001$); however, it had no significant effect on the leaves fresh weight (Fig. 1a), $p = 0.784$), leaves dry weight (Fig. 1b), $p = 0.791$), root length (Fig. 1c), $p = 0.116$) and stomatal conductance (Fig. 1g), $p = 0.059$) in *S. canadensis*. Salt treatments significantly reduced the plant height by 5.48 and 18.17%, seedling dry weight by 19.03 and 28.75%, water use efficiency by 22.81 and 21.65%, intracellular $CO_2$ by 4.48 and 20.71%, and net photosynthetic rate by 13.54 and 35.44% respectively under moderate (100 mM NaCl) and severe salinity (150 mM NaCl) stress than control plants.

### Effect of Drought Stress on Growth and Physiological Traits

Drought stress had a significant effect on leaves fresh weight (Fig. 2a) $p = 0.001$), leaves dry weight (Fig. 2b), $p = 0.001$), plant height (Fig. 2d), $p = 0.001$), stomatal conductance (Fig. 2h), $p = 0.001$) and net photosynthetic rate (Fig. 2i), $p = 0.001$); however, it had no significant effect on the root length (Fig. 2c), $p = 0.264$), seedling dry weight (Fig. 2e, $p = 0.350$), water use efficiency (Fig. 2f), $p = 0.131$), and intracellular $CO_2$ (Fig. 2g), $p = 0.504$) in *S. canadensis*. Drought treatments significantly reduced the leaves fresh weight, leaves dry weight, plant height, stomatal conductance,

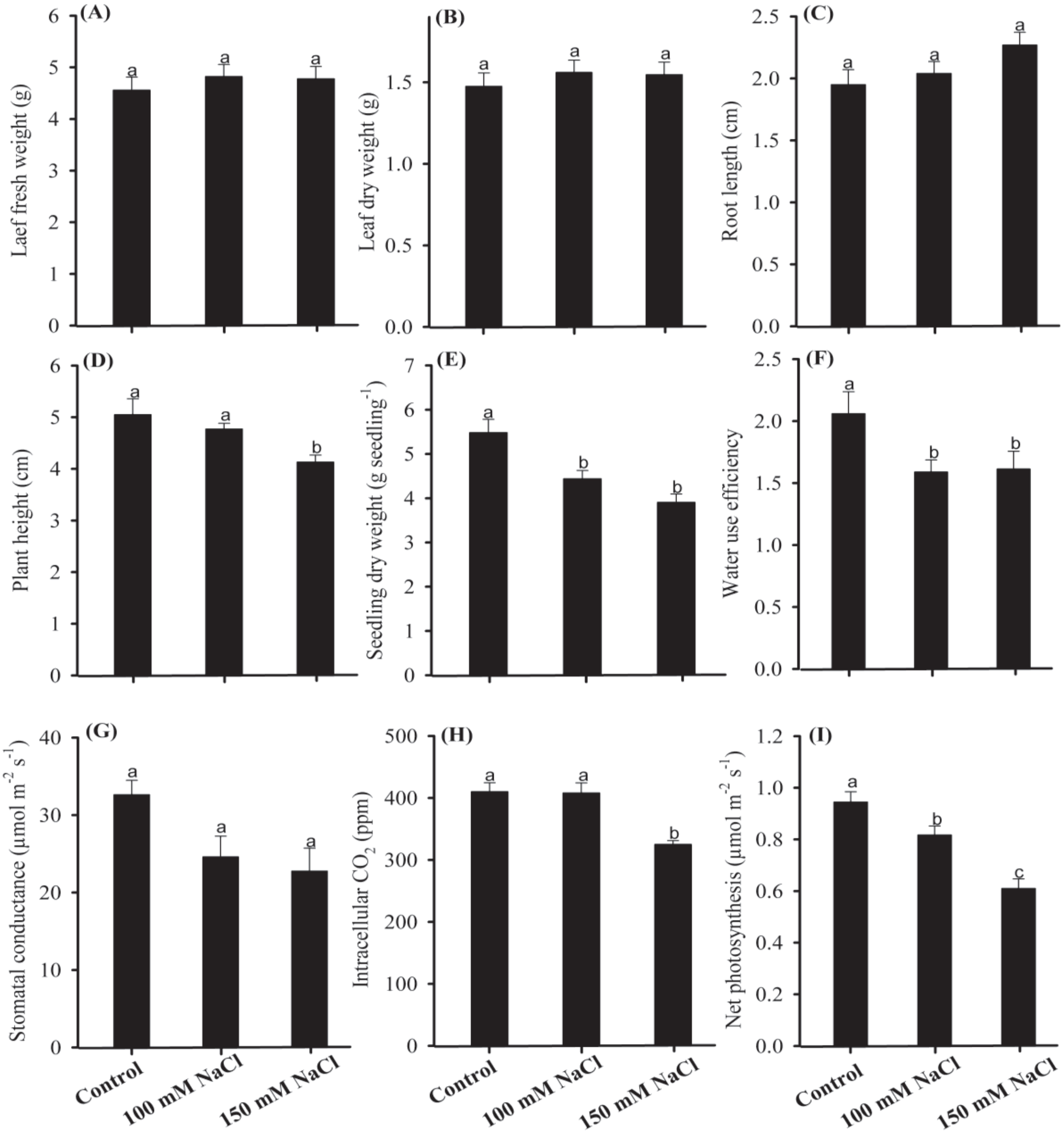

Fig. 1. Leaves fresh a) and dry weights b), root length c), plant height d), seedling dry weight e), water use efficiency f), stomatal conductance g), intracellular $CO_2$ h), and net photosynthetic rate i) in *S. canadensis* plants exposed to salt treatments. The data are presented as the means±SE, n = 12. Similar letters above bars indicate no significant differences among treatments at ($p$<0.05).

and net photosynthetic rate with maximum decrease under severe drought stress, where the value was 31.01%, 30.39%, 35.09%, 49.19%, and 46.93% lower respectively than control plants (no drought application).

## Effect of Abscisic Acid Application on Growth and Physiological Traits

Abscisic acid application had no significant influence on the leaves fresh weight (Fig. 3a), $p$ = 0.217), leaves dry weight (Fig. 3b), $p$ = 0.216), root length (Fig. 3c), $p$ = 0.778), plant height (Fig. 3d), $p$ = 0.952), seedling dry weight (Fig. 3e), $p$ = 0.847), water use efficiency (Fig. 3f), $p$ = 0.119), intracellular $CO_2$ (Fig. 3h), $p$ = 0.888), stomatal conductance (Fig. 3g, $p$ = 0.270) and net photosynthetic rate (Fig. 3i), $p$ = 0.190) in *S. canadensis*.

## Discussion

Previous studies have reported a detrimental effect of drought and salt stress on plants, especially affecting the growth and physiological traits [4, 38, 39]. In a recent study, Li et al. [5] reported that salt stress significantly affected different physiological traits (number of leaves, plant height, the root, shoot, and total biomass), net photosynthetic rate, stomatal conductance,

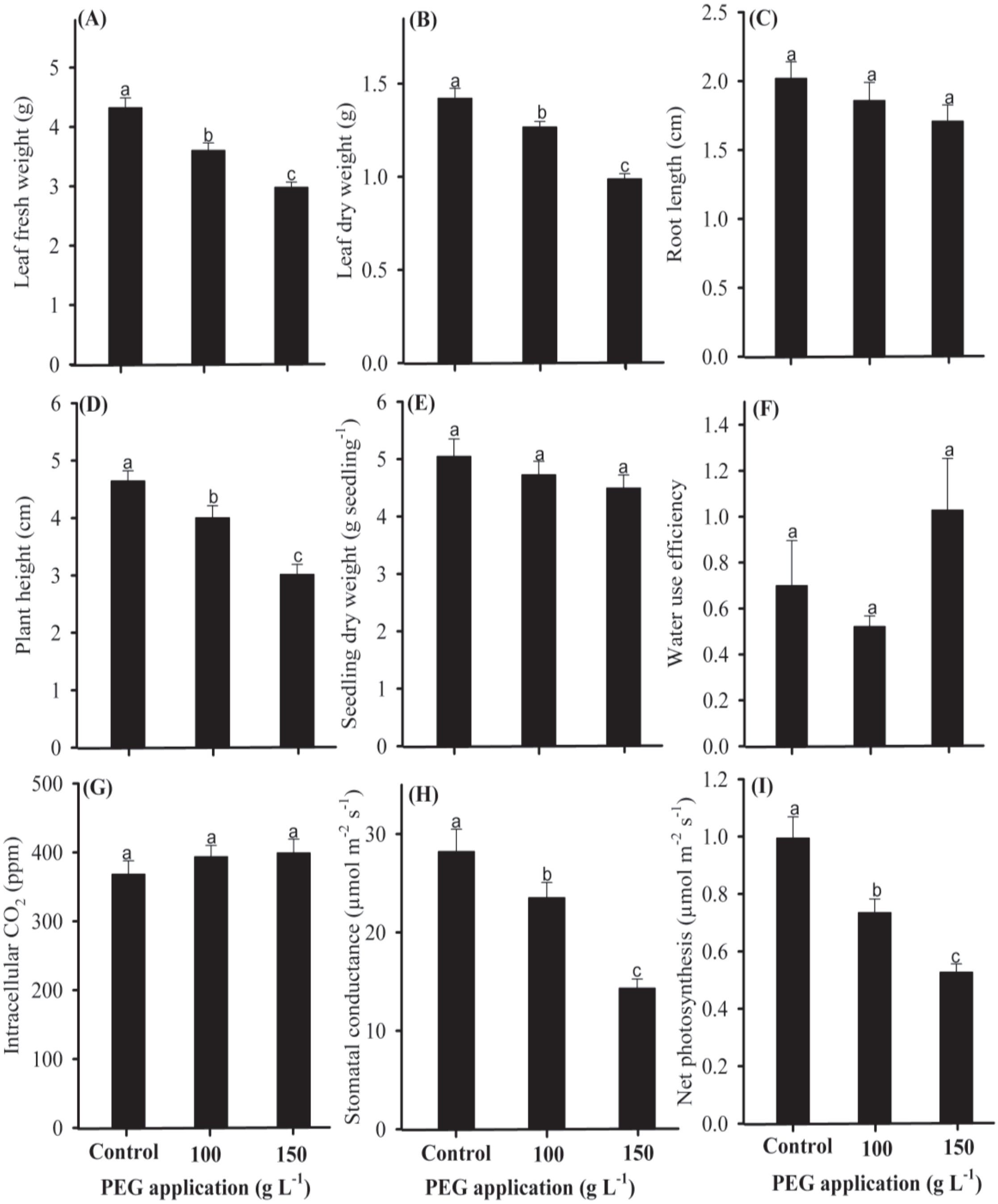

Fig. 2. Leaves fresh a) and dry weights b), root length c), plant height d), seedling dry weight e), water use efficiency f), intracellular $CO_2$ g), stomatal conductance h), and net photosynthetic rate i) in *S. canadensis* plants exposed to drought stress. The data are presented as the means±SE, n = 12. Similar letters above bars indicate no significant differences among treatments at ($P<0.05$).

transpiration rate, and relative chlorophyll content of *S. canadensis* under greenhouse experiment. Similarly, in this study, we found that salinity treatments have a detrimental effect on the plant height, seedling dry weight, water use efficiency, and physiological traits, including net photosynthesis rates and intracellular $CO_2$ concentrations in *S. canadensis.* These results suggest that different salinity treatments significantly affect plant growth and developmental characteristics and suggesting that *S. canadensis* shows a mild local adaptation to salt stress in China. These findings are consistent with Li et al. [5], where the authors have reported a lack of evidence for local adaptation of *S. canadensis* to different salinity stress levels in China. However, inconsistent with our results, various studies have documented that invasive plant species have a more remarkable ability to adapt the heterogeneous environments [40, 41].

Furthermore, in our study, drought treatments also influenced *S. canadensis* growth and physiological

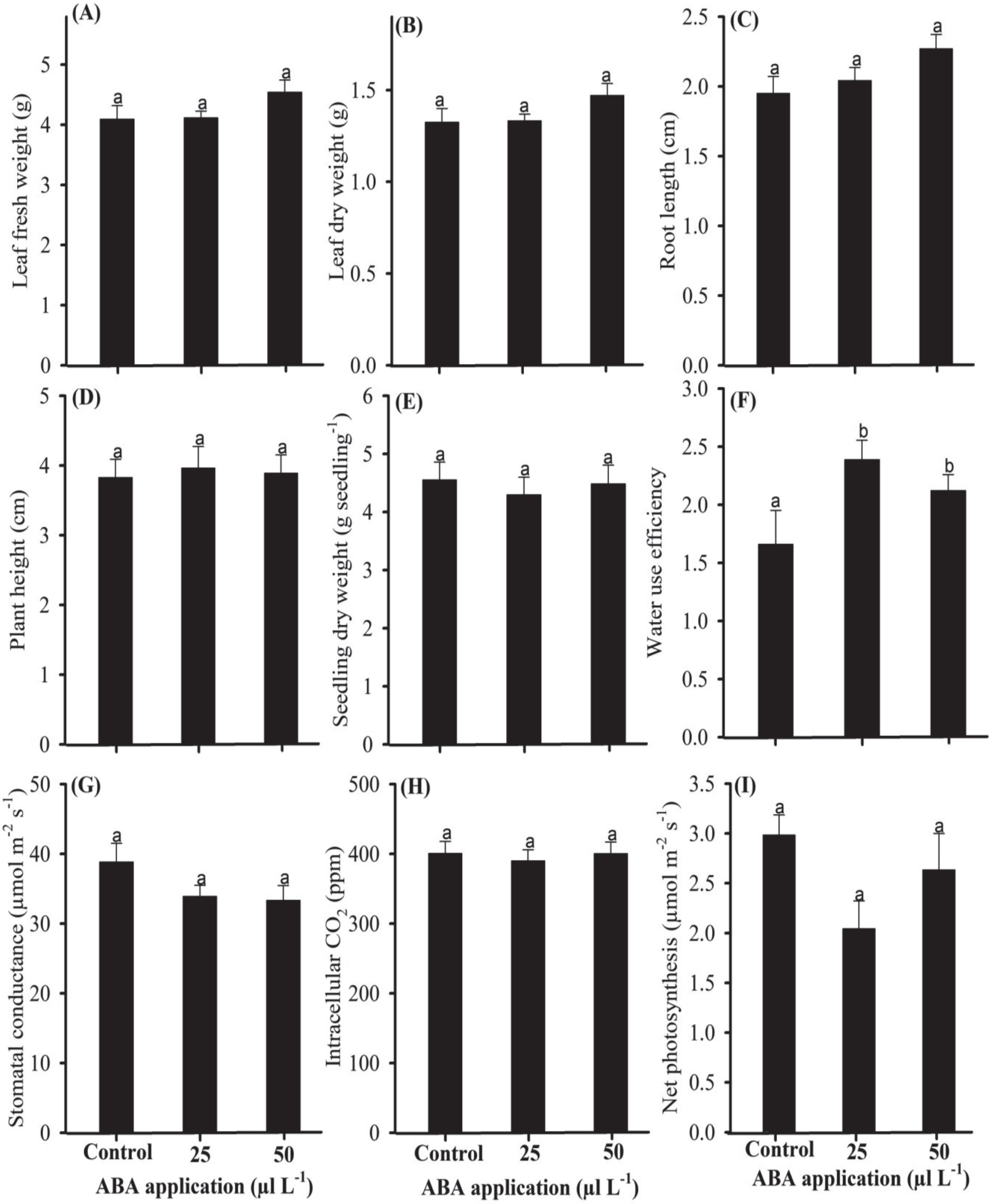

Fig. 3. Influence of abscisic acid (ABA) application on the leaves fresh a) and dry weights b), root length c), plant height d), seedling dry weigh e), water use efficiency f), stomatal conductance g), intracellular $CO_2$ h), and net photosynthetic rate i) in *S. canadensis* plants. The data are presented as the means c±SE, n = 12. Similar letters above bars indicate no significant differences among treatments at ($p$<0.05).

traits, suggesting lower adaptability to drought conditions. These findings are consistent with previous results of Du et al. [42], where the authors have reported that drought stress significantly reduced the growth, and physiological traits, including photosynthesis rates of invasive plants. Inconsistent with our results, the deleterious effect of environmental stresses on the performance of *S. canadensis* was also reported in previous studies [43, 44]. Plasticity contributes to the successful adaptation of invasive species to heterogeneous environments [10, 45, 46]. Furthermore, local adaptation also plays a central role in biological invasion and contributes to a wide distribution across diverse habitats [9, 47]. In this study, salinity and drought stresses significantly reduced the performance of *S. canadensis*, suggesting a mild local adaptation to these stresses. These findings are inconsistent with previously published studies, where the authors have reported a shred of solid evidence for local adaptation of invasive plants [5, 9]. In a recent study, Jin et al. [48] reported a partial local adaptation in *S. canadensis* to a low salinity level. Working with invasive *Wedelia trilobat*, adopt local adaptation occurred in light conditions [14]. Similarly, *Senecio inaequidens* also reported the local adaptation of species on a small scale [14]. Under adequate water supply, physiological traits, including high photosynthetic rates, significantly contribute to the success and spread of *Chromolaena odorata* [49].

Our results also indicated that salinity treatments reduced the plant height, seedling dry weight, water use efficiency, intracellular $CO_{2,}$ and net photosynthetic rates in *S. canadensis* plants, suggesting that *S. canadensis* plants exhibit some degree of phenotypic plasticity under salt stress conditions. Similar findings were also reported by Jin et al. [48]; *S. canadensis* seeds exhibit a partial degree of phenotypic plasticity under the saline environment. In another study, there was a no evidence for local adaptation in growth and physiological traits of *Hordeum spontaneum* populations from high saline region of northern China [50]. Plasticity in drought stress significantly contributes to widespread distribution of *Leymus Chinensis* plant to occupy a wide range of environments [51]. Furthermore, drought stress also reduced the plant height, leaves fresh and dry weights, stomatal conductance, and net photosynthetic rate in *S. canadensis* plants, showing a partial degree of phenotypic plasticity (Fig. 2). Overall, these results suggest that *S. canadensis* plants showed a lower local adaptation to salinity and drought stress. The growth and physiological traits have remained significantly affected by these stresses.

In this study, for the first time, we have reported the performance of invasive *S. canadensis* plants under ABA application. In our work, ABA application had no significant influence on the growth measures and physiological traits of *S. canadensis* (Fig. 3). Previously, the study reported that most invasive species' seedling growth is significantly inhibited under ABA application [52]. In contrast to our findings, the improved plant growth under ABA application has been well documented in various published studies [53].

## Conclusion

Salinity and drought treatments showed mild influence on the growth and physiological traits of *S. canadensis*, excluding in leaves fresh and dry weight, root length, and stomatal conductance under salinity stress, and root length, dry seedling weight, water use efficiency, and intracellular $CO_2$ under drought stress. These findings indicated that local adaptation is less critical than individual plasticity in affecting the growth, physiological traits, salinity, and drought stress response of *S. canadensis*.

## Acknowledgments

This work was supported by the National Natural Science Foundation of China (32071521, 31770446, 31200316), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), the Jiangsu Collaborative Innovation Centre of Technology and Material of Water Treatment, Study Abroad Scholarship of Jiangsu University, Senior Talent Fund of Jiangsu University (11JDG150).

## Conflict of Interest

The authors declare no conflict of interest.

## References

1. MOLLOT G., PANTEL J., ROMANUK T. The effects of invasive species on the decline in species richness: a global meta-analysis. Adv. Ecol. Res. **56**, 61, **2017**.
2. SAHA M., WIESE J., WEINBERGER F., WAHL M. Rapid adaptation to controlling new microbial epibionts in the invaded range promotes invasiveness of an exotic seaweed. J. Ecol. **104**, 969, **2016**.
3. CHEN D., ALI A., YONG X.H., LIN C.G., NIU X.H., CAI A.M., DONG B.C., ZHOU Z.X., WANG Y.J., YU F.H. A multi-species comparison of selective placement patterns of ramets in invasive alien and native clonal plants to light, soil nutrient and water heterogeneity. Sci. Total Environ. **657**, 1568, **2019**.
4. WANG Y.J., MÜLLER-SCHÄRER H., VAN KLEUNEN M., CAI A.M., ZHANG P., YAN R., DONG B.C., YU F.H. Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives. New Phytol. **216**, 1072, **2017**.
5. LI J., LIU H., YAN M., DU L. No evidence for local adaptation to salt stress in the existing populations of invasive *Solidago canadensis* in China. PLoS One **12**, e0175252, **2017**.
6. ANDERSON J., WAGNER M., RUSHWORTH C., PRASAD K., MITCHELL-OLDS T. The evolution of quantitative traits in complex environments. Heredity **112**, 4, **2014**.
7. ODUOR A.M., LEIMU R., VAN KLEUNEN M. Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. J. Ecol. **104**, 957, **2016**.
8. WOODS H.A., PINCEBOURDE S., DILLON M.E., TERBLANCHE J.S. Extended phenotypes: buffers or amplifiers of climate change? Trends Ecol. Evol. **2021**.
9. COLAUTTI R.I., LAU J.A. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. Mol. Ecol. **24**, 1999, **2015**.

10. GRATANI L. Plant phenotypic plasticity in response to environmental factors. Adv. Bot. 2014, **2014**.
11. MATESANZ S., RAMOS-MUÑOZ M., MONCALVILLO B., RUBIO TESO M., GARCÍA DE DIONISIO S., ROMERO J., IRIONDO J. Plasticity to drought and ecotypic differentiation in populations of a crop wild relative. AoB Plants **12**, plaa006, **2020**.
12. LITCHMAN E. Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. Ecol. Lett. **13**, 1560, **2010**.
13. TE BEEST M., LE ROUX J.J., RICHARDSON D.M., BRYSTING A.K., SUDA J., KUBEŠOVÁ M., PYŠEK P. The more the better? The role of polyploidy in facilitating plant invasions. Ann. Bot. **109**, 19, **2012**.
14. SI C.-C., DAI Z.-C., LIN Y., QI S.-S., HUANG P., MIAO S.-L., DU D.-L. Local adaptation and phenotypic plasticity both occurred in Wedelia trilobata invasion across a tropical island. Biol. Invasions **16**, 2323, **2014**.
15. REGER J., LIND M.I., ROBINSON M.R., BECKERMAN A.P. Predation drives local adaptation of phenotypic plasticity. Nat. Ecol. Evol. **2**, 100, **2018**.
16. SHEN X.-Y., PENG S.-L., CHEN B.-M., PANG J.-X., CHEN L.-Y., XU H.-M., HOU Y.-P. Do higher resource capture ability and utilization efficiency facilitate the successful invasion of native plants? Biol Invasions **13**, 869, **2011**.
17. ROUIFED S., BYCZEK C., LAFFRAY D., PIOLA F. Invasive knotweeds are highly tolerant to salt stress. Environ. Manag. **50**, 1027, **2012**.
18. CHEN H., JIANG J.-G. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environ. Rev. **18**, 309, **2010**.
19. EVELIN H., DEVI T.S., GUPTA S., KAPOOR R. Mitigation of salinity stress in plants by arbuscular mycorrhizal symbiosis: current understanding and new challenges. Front. Plant Sci. **10**, 470, **2019**.
20. FAHAD S., HUSSAIN S., MATLOOB A., KHAN F.A., KHALIQ A., SAUD S., HASSAN S., SHAN D., KHAN F., ULLAH N. Phytohormones and plant responses to salinity stress: a review. Plant Growth Regul. **75**, 391, **2015**.
21. SAFDAR H., AMIN A., SHAFIQ Y., ALI A., YASIN R., SHOUKAT A., HUSSAN M.U., SARWAR M.I. A review: Impact of salinity on plant growth. Nat. Sci. **17**, 34, **2019**.
22. ÁLVAREZ S., SANCHEZ-BLANCO M. Long-term effect of salinity on plant quality, water relations, photosynthetic parameters and ion distribution in *Callistemon citrinus*. Plant Biol. **16**, 757, **2014**.
23. HUSSAIN T., KOYRO H.-W., ZHANG W., LIU X., GUL B., LIU X. Low Salinity Improves Photosynthetic Performance in Panicum antidotale Under Drought Stress. Front. Plant Sci. **11**, 481, **2020**.
24. LOWRY D.B., HALL M.C., SALT D.E., WILLIS J.H. Genetic and physiological basis of adaptive salt tolerance divergence between coastal and inland Mimulus guttatus. New Phytol.**183**, 776, **2009**.
25. PAZZAGLIA J., REUSCH T. B., TERLIZZI A., MARÍ-GUIRAO L., PROCACCINI G. Phenotypic plasticity under rapid global changes: The intrinsic force for future seagrasses survival. Evol. Appl. **14**, 1181, **2021**.
26. VASQUEZ E.A., GLENN E.P., GUNTENSPERGEN G.R., BROWN J.J., NELSON S.G. Salt tolerance and osmotic adjustment of Spartina alterniflora (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. Am. J. Bot. **93**, 1784, **2006**.
27. KUHN N.L., ZEDLER J.B. Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. Estuaries **20**, 391, **1997**.28.
28. AL HASSAN M., CHAURA J., LÓPEZ-GRESA M.P., BORSAI O., DANISO E., DONAT-TORRES M.P., MAYORAL O., VICENTE O., BOSCAIU M. Native-invasive plants vs. halophytes in Mediterranean salt marshes: stress tolerance mechanisms in two related species. Front. Plant Sci. **7**, 473, **2016**.
29. CHIRINO E., RUIZ-YANETTI S., VILAGROSA A., MERA X., ESPINOZA M., LOZANO P. Morpho-functional traits and plant response to drought conditions in seedlings of six native species of Ecuadorian Ecosystems. Flora **233**, 58, **2017**.
30. RADHAKRISHNAN R., PARK J.-M., LEE I.-J. *Enterobacter* sp. I-3, a bio-herbicide inhibits gibberellins biosynthetic pathway and regulates abscisic acid and amino acids synthesis to control plant growth. Microbiol. Res. **193**, 132, **2016**.
31. VISHAL B., KUMAR P.P. Regulation of seed germination and abiotic stresses by gibberellins and abscisic acid. Front. Plant Sci. **9**, 838, **2018**.
32. MEI D., JIAN-ZHONG L., WEN-JU Z., JIA-KUAN C., BO L. Canada goldenrod (*Solidago canadensis*): an invasive alien weed rapidly spreading in China. Journal of Systematics and Evolution **44**, 72, **2006**.
33. JIAN-ZHONG L., EN-SHENG W., XIAO-WEN W., WEBER E., BIN Z., BO L. Potential distribution of Solidago canadensis in China. J. Syst. Evol. **45**, 670, **2007**.
34. LI J., DU L., GUAN W., YU F.-H., VAN KLEUNEN M. Latitudinal and longitudinal clines of phenotypic plasticity in the invasive herb *Solidago canadensis* in China. Oecologia **182**, 755, **2016**.
35. DU L., LIU H., YAN M., LI J., LI J. Individual plasticity of the shade response of the invasive *Solidago canadensis* in China. PloS One **12**, e0170049, **2017**.
36. ZHU L. Distribution and ecological adaptation characteristics of *Solidago canadensis* to Jiuduansha, Shanghai. Master degree thesis of Shanghai Normal University **2012**.
37. HOAGLAND D.R., ARNON D.I. The water-culture method for growing plants without soil. Calif. Agric. Exp. Stn. Circ. **1950**.
38. LOGOFET D.O., ULANOVA N.G., BELOVA I.N. Adaptation on the ground and beneath: does the local population maximize its λ1? Ecol. Complex. **20**, 176, **2014**.
39. REN Y., WANG W., HE J., ZHANG L., WEI Y., YANG M. Nitric oxide alleviates salt stress in seed germination and early seedling growth of pakchoi (*Brassica chinensis* L.) by enhancing physiological and biochemical parameters. Ecotoxicol. Environ. Saf. **187**, 109785, **2020**.
40. GENG Y., VAN KLINKEN R. D., SOSA A., LI B., CHEN J., XU C.-Y. The relative importance of genetic diversity and phenotypic plasticity in determining invasion success of a clonal weed in the USA and China. Front. Plant Sci. **7**, 213, **2016**.
41. VANWALLENDAEL A., HAMANN E., FRANKS S.J. Evidence for plasticity, but not local adaptation, in invasive Japanese knotweed (*Reynoutria japonica*) in North America. Evol. Ecol. **32**, 395, **2018**.
42. DU L., LIU H., GUAN W., LI J., LI J. Drought affects the coordination of belowground and aboveground resource-related traits in Solidago canadensis in China. Ecol. Evol. **9**, 9948, **2019**.
43. DAS A., PARIDA K. Salt tolerance and salinity affect on plants a review. Ecotoxicol. Environ. Saf. **60**, 324, **2005**.

44. SCHITTKO C., WURST S. Above-and belowground effects of plant-soil feedback from exotic Solidago canadensis on native Tanacetum vulgare. Biol. Invasions **16**, 1465, **2014**.
45. CANO L., ESCARRÉ J., FLECK I., BLANCO-MORENO J., SANS F. Increased fitness and plasticity of an invasive species in its introduced range: a study using Senecio pterophorus. J. Ecol. **96**, 468, **2008**.
46. ZENNI R.D., LAMY J.-B., LAMARQUE L. J., PORTÉ A.J. Adaptive evolution and phenotypic plasticity during naturalization and spread of invasive species: implications for tree invasion biology. Biol. Invasions **16**, 635, **2014**.
47. YOSHIDA T., CHRISTMANN A., YAMAGUCHI-SHINOZAKI K., GRILL E., FERNIE A.R. Revisiting the basal role of ABA-roles outside of stress. Trends Plant Sci. **24**, 625, **2019**.
48. JIN H., YUAN Y., GAO F., ODUOR A.M., LI J. The invasive plant Solidago canadensis exhibits partial local adaptation to low salinity at germination but not at later life-history stages. Am. J. Bot. **107**, 599, **2020**.
49. NAIDOO G., NAIDOO K. Drought stress effects on gas exchange and water relations of the invasive weed Chromolaena odorata. Flora **248**, 1, **2018**.
50. VOLIS S., MENDLINGER S., WARD D. Adaptive traits of wild barley plants of Mediterranean and desert origin. Oecologia **133**, 131, **2002**.
51. LIU Y., ZHANG L., XU X., NIU H. Understanding the wide geographic range of a clonal perennial grass: plasticity versus local adaptation. AoB Plants **8**, **2016**.
52. LIU J., WANG W., WANG L., SUN Y. Exogenous melatonin improves seedling health index and drought tolerance in tomato. Plant Growth Regul. **77**, 317, **2015**.
53. TINCANI M., TRAVERS J. Replication research, publication bias, and applied behavior analysis. Perspect. Behav. Sci. **42**, 59, **2019**.