Plant Physiology and Biochemistry 95 (2015) 41–48

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Salinity affects production and salt tolerance of dimorphic seeds of *Suaeda salsa*

Fengxia Wang [a], Yan-ge Xu [a], Shuai Wang [a], Weiwei Shi [a], Ranran Liu [a], Gu Feng [b], Jie Song [a,*]

[a] *Key Laboratory of Plant Stress, College of Life Science, Shandong Normal University, Jinan 250014, PR China*
[b] *College of Resource and Environmental Science, China Agricultural University, Beijing 100094, PR China*

ARTICLE INFO

Article history:
Received 9 May 2015
Received in revised form 30 June 2015
Accepted 1 July 2015
Available online 6 July 2015

Keywords:
Endogenous hormone
Germination
Salinity
Seed development
Seed dimorphism
Suaeda salsa

ABSTRACT

The effect of salinity on brown seeds/black seeds ratio, seed weight, endogenous hormone concentrations, and germination of brown and black seeds in the euhalophyte *Suaeda salsa* was investigated. The brown seeds/black seeds ratio, seed weight of brown and black seeds and the content of protein increased at a concentration of 500 mM NaCl compared to low salt conditions (1 mM NaCl). The germination percentage and germination index of brown seeds from plants cultured in 500 mM NaCl were higher than those cultured in 1 mM NaCl, but it was not true for black seeds. The concentrations of IAA (indole-3-acetic acid), ZR (free zeatin riboside) and ABA (abscisic acid) in brown seeds were much greater than those in black seeds, but there were no differences in the level of GAs (gibberellic acid including GA_1 and GA_3) regardless of the degree of salinity. Salinity during plant culture increased the concentration of GAs, but salinity had no effect on the concentrations of the other three endogenous hormones in brown seeds. Salinity had no effect on the concentration of IAA but increased the concentrations of the other three endogenous hormones in black seeds. Accumulation of endogenous hormones at different concentrations of NaCl during plant growth may be related to seed development and to salt tolerance of brown and black *S. salsa* seeds. These characteristics may help the species to ensure seedling establishment and population succession in variable saline environments.

1. Introduction

It is estimated that over 800 million hectares of land are salt-affected throughout the world (Munns, 2005). Meanwhile, global annual losses in agricultural production from salt-affected land are in excess of US$12 billion and rising (Shabala, 2013). Therefore, it has become imperative to identify plants with high economic value that can grow under high salt conditions. *Suaeda salsa* L. is a leaf-succulent halophytic herb with high salt tolerance during germination and seedling stages. Recently, it was suggested that *S. salsa* should be *Suaeda maritima* subsp. *salsa* (L.) Soó. It was also suggested that the species used in the present study may be *Suaeda liaotungensis* Kit. Therefore, the nomenclature and taxonomic position of the study species need to be identified (*S. salsa* was still used in the present study). *S. salsa* seeds germinate in late April. The plants flower from July onwards, and seeds begin to mature in late September (Song and Wang, 2015). Nowadays, the species is economically important because its fresh branches have high value as a vegetable and its seed oil is edible and rich in unsaturated fatty acids. Moreover, because the plant is capable of removing salts and heavy metals from saline soils, *S. salsa* can also be used in the restoration of heavily-salinized land (Song and Wang, 2015).

Seed dimorphism and polymorphism within a plant refers to there being different seeds whose morphological structure and physiological properties are different from each other. Seed dimorphism is a powerful germination strategy in unpredictable environments, such as deserts and high salt soil areas (Wang et al., 2010). Currently, studies of seed dimorphism have become important for understanding plant adaptability (Wei et al., 2007; Yao et al., 2010). Seed dimorphism and polymorphism exists in halophytes such as *Suaeda moquinii* (Khan et al., 2001) and *Salsola affinis* (Wei et al., 2007). *S. salsa* also produces dimorphic seeds, i.e., some seeds are brown and have a soft outer seed coat (big seed), and

Abbreviations: IAA, indole-3-acetic acid; ZR, zeatin riboside; ABA, abscisic acid; GA, gibberellic acid.

* Corresponding author. Wenhua East Road 88, Jinan 250014, PR China.
E-mail address: songjieever@163.com (J. Song).

http://dx.doi.org/10.1016/j.plaphy.2015.07.005
0981-9428/

other seeds are black and have a hard and smooth outer seed coat (small seed) (Li et al., 2005; Song et al., 2008). Cytokinins (CTKs), indole-3-acetic acid (IAA) and gibberellic acid (GA) are important hormones which play crucial roles in regulating the cell cycle, proliferation and differentiation of plant cells (Rijavec et al., 2009; Uchiumi and Okamoto, 2010). However, it is not clear whether these hormones are related to seed development in dimorphic seeds of *S. salsa*. Brown seeds have a higher salt tolerance than black seeds, for example the 50% inhibition of germination was achieved for black seeds between 300 and 400 mM NaCl and between 600 and 800 mM NaCl for brown seeds (Li et al., 2005). It has been reported that certain hormones such as cytokinin (CTK) and auxin (i.e., IAA) can increase the salt tolerance of seeds in certain plant species (Park et al., 2011). It is also still unclear whether these hormones are related to seed salt tolerance in dimorphic seeds of *S. salsa*.

Germination is pivotal to plant establishment (Wang et al., 2015). A high salt concentration in the soil prevents germination, and seeds only germinate when temperature and edaphic conditions become favorable (Ungar, 1996; Khan and Ungar, 1997; Tessier et al., 2000). Seeds of halophytes and nonhalophytes respond similarly to salinity stress. For instance, the initial germination process is delayed under salt stress (Almansouri et al., 2001; Khajeh-Hosseini et al., 2003). Besides salinity, plant growth regulators also affect seed germination and dormancy under high salt conditions.

Former reports indicated that salt tolerance of brown seeds and young seedlings from brown seeds of *S. salsa*, cultivated under high salinity, were greater than when cultivated under low salinity because salinity during seed maturation may increase the contents of amino acids in the embryos of the maturing brown seeds (Li, 2012) and by changing the lipid composition of membranes in mature brown seeds (Zhou et al., 2014). However, there is no information describing how salinity during plant culture affects brown seeds/black seeds ratio, the salt tolerance of black seeds, and endogenous hormone concentrations in dimorphic seeds of *S. salsa*. The present study investigated these aspects in an attempt to further understand how *S. salsa* adapted to variable saline environments during both seed production and germination stages.

2. Results

2.1. Morphology of seeds

Both seeds and embryos of mature brown and black seeds from plants cultured at 500 mM NaCl were better developed than those from plants cultured at 1 mM NaCl (Fig. 1).

2.2. The brown seeds/black seeds ratio and seed weight

In a previous experiment, we found that *S. salsa* as an euhalophyte can not grow well without NaCl. Therefore, normally 1 mM NaCl rather than 0 mM NaCl was used as control during plant culture of the species. The brown seeds/black seeds ratio was 1.8 times greater at 500 mM NaCl than that at 1 mM NaCl during plant culture (Fig. 2A). Brown seed weight was higher than black seed weight regardless of the salinity. Salinity increased seed weight regardless of seed type, e.g., the seed weight of brown and black seeds at 500 mM NaCl was 1.6 and 1.9 times of that at 1 mM NaCl, respectively (Fig. 2B, Table 1).

2.3. The protein content in brown and black seeds

The protein content in brown seeds was 1.8 and 1.9 times of that in black seeds at 1 and 500 mM NaCl during plant culture, respectively. Salinity had no significant effect on the protein content of brown and black seeds (Fig. 2C, Table 1).

2.4. Germination index, final germination and total germination

In general, non-halophytes and halophytes respond to salinity in a similar way during the germination stage; the initial germination process is delayed under salt stress (Khan and Ungar, 1997; Li et al., 2005), i.e., unlike plant culture, salinity was not necessary during germination. Therefore, 0 mM NaCl was used as control during seed germination in the present experiment. The germination index of brown seeds harvested from plants cultured at 1 or 500 mM NaCl was higher than that of black seeds at 0 or 600 mM NaCl during germination (Fig. 3A, Table 2). Salinity decreased the germination index of brown and black seeds but more significantly in black seeds. The germination index of brown seeds from plants cultured at 500 mM NaCl was higher than at 1 mM NaCl, and even higher when germination conditions were 600 mM NaCl. The value for brown seeds from plants cultured at 500 mM NaCl was 1.5 and 2.8 times of that from plants cultured at 1 mM NaCl at germination conditions of 0 and 600 mM NaCl, respectively. The opposite trend was observed in black seeds (Fig. 3A, Table 2). The final germination values followed the same trend as the germination index (Fig. 3B, Table 2).

High salinity (600 mM NaCl) had no adverse effects on the total germination of brown seeds from plants cultured at both 1 and 500 mM NaCl after un-germinated brown seeds were pretreated with 600 mM NaCl and transferred to 0 mM NaCl, but a concentration of 600 mM NaCl decreased the total germination of black seeds regardless of the NaCl concentration during plant culture. The total germination of black seeds from plants cultured at 500 mM NaCl was lower than that at 1 mM NaCl regardless of NaCl concentrations during germination. For example, total germination of black seeds from plants cultured at 500 mM NaCl was 69.4% at 0 mM NaCl during germination and 76.9% at 600 mM NaCl during germination compared to plants cultured at 1 mM NaCl, respectively (Fig. 3C, Table 2).

2.5. Endogenous hormone concentration

The concentrations of IAA, ZR and ABA in brown seeds were much higher than those in black seeds, but there was no difference in GAs levels (Fig. 4, Table 2). Salinity during plant culture increased the concentration of GAs, but salinity had no effect on the concentrations of the other three endogenous hormones in brown seeds. Salinity had no effect on the concentration of IAA but increased the concentrations of the other three endogenous hormones in black seeds (Fig. 4, Table 1).

3. Discussion

In the course of evolution, the ability of certain plant species to produce heteromorphic seeds has been mostly observed in species found in semi-arid, saline-rich and other unfavorable environments (Imbert, 2002). Seed heteromorphism is often considered a bet-hedging strategy to ensure seedling establishment and population succession for certain plant species in areas with high seasonal fluctuations. *Chenopodium album* plants that suffered higher salinity stress produced more salt-resistant seeds (brown seeds); brown seeds were larger and more salt tolerant than black seeds, and could germinate more rapidly in a wider range of environments (Yao et al., 2010). High levels of salinity did not change the seed morph ratio in *Suaeda aralocaspica* (Wang et al., 2012a). In the present study, salinity increased the brown seeds/black seeds ratio (Fig. 2A). The salt content in saline soils where *S. salsa* growth