



Research article

Effects of non-uniform root zone salinity on growth, ion regulation, and antioxidant defense system in two alfalfa cultivars

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ARTICLE INFO

Keywords:

Alfalfa
Non-uniform salinity
Split-root system
Na⁺ efflux
Antioxidant defense

ABSTRACT

A split-root system was established to investigate the effects of uniform (0/0, 50/50, and 200/200 mM salt [NaCl]) and non-uniform (0/200 and 50/200 mM NaCl) salt stress on growth, ion regulation, and the antioxidant defense system of alfalfa (*Medicago sativa*) by comparing a salt-tolerant (Zhongmu No.1) and salt-sensitive (Algonquin) cultivar. We found that non-uniform salinity was associated with greater plant growth rate and shoot dry weight, lower leaf Na⁺ concentration, higher leaf potassium cation (K⁺) concentration, lower lipid peroxidation, and greater superoxide dismutase (EC 1.15.1.1), catalase (EC 1.11.1.6), and peroxidase (EC 1.11.1.7) activities, compared to uniform salt stress in both alfalfa cultivars. Under non-uniform salinity, a significant increase in Na⁺ concentration and Na⁺ efflux and a decline in K⁺ efflux in the no-saline or low-saline part of the roots alleviated salt damage. Our results also demonstrated that proline and antioxidant enzymes accumulated in both the no- or low-saline and high-saline roots, revealing that osmotic adjustment and antioxidant defense had systemic rather than localized effects in alfalfa plants, and there was a functional equilibrium within the root system under non-uniform salt stress. The salt-tolerant cultivar Zhongmu No.1 exhibited greater levels of growth compared to Algonquin under both uniform and non-uniform salt stress, with Na⁺ tolerance and efflux abilities more effective and greater antioxidant defense capacity evident for cultivar Zhongmu No.1.

1. Introduction

Soil salinization is a global problem that significantly limits plant growth and food production. The spatial variation of soil salinity is mainly affected by the interactions between environmental factors, such as microtopography, climate, soil properties, irrigation, and fertilization, which induce salinity non-uniformly in the soil in both space and time (Bazihizina et al., 2012; Guo et al., 2015b; Valdés et al. 2014, 2015; Wang et al., 2008; Yang et al., 2016). The range in soil salinity experienced by roots can be large, even within the root zone of single plants (Bazihizina et al., 2012; Li et al., 2010). Therefore, most recent studies have focused on the response of plants to non-uniform salinity in a single root zone (Chen et al., 2016; Feng et al., 2017; Kong et al.

2012, 2017, 2016; Koushafar et al., 2011; Nadia et al., 2012; Sun et al., 2016). Using a split-root system, a section of the root can be isolated from the entire whole root system and subjected to different sodium chloride (NaCl) treatments while maintaining a shared conjunct aerial part (Bazihizina et al., 2009; Kong et al., 2012; Larrainzar et al., 2014; Sonneveld and Kreij, 1999). Studies have indicated that compared to uniform salt stress, non-uniform salinity can alleviate the damage caused by salt stress to plants, as observed in cucumber (Sonneveld and Kreij, 1999), tomato (Koushafar et al., 2011), cotton (Dong et al., 2010a), *Atriplex nummularia* (Bazihizina et al., 2009), alfalfa (Sun et al., 2016), and *Lycium chinense* (Feng et al., 2017). However, the salt tolerance mechanisms of plants under non-uniform salt stress remain largely undetermined.

Abbreviations: CAT, catalase; Chl, chlorophyll; DW, dry weight; HKT1, high-affinity potassium transporter; H₂O₂, hydrogen peroxide; MDA, malondialdehyde; NMT, non-invasive micro-test technology; POD, peroxidase; Pro, proline; ROS, reactive oxygen species; SOD, superoxide dismutase; SOS, salt overly sensitive

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<https://doi.org/10.1016/j.plaphy.2018.09.028>

Received 23 April 2018; Received in revised form 31 August 2018; Accepted 20 September 2018

Available online 21 September 2018

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When a plant is exposed to saline soil, it is first subjected to osmotic stress, which immediately influences water uptake and plant growth (Liang et al., 2018; Munns and Tester, 2008). Plants have developed a set of physiological mechanisms to cope with salt stress. Many studies have confirmed that water uptake by plants under non-uniform salinity is greater than under uniform salt stress. This is because most of the water uptake originates from the no- or low-saline parts of the root zone (Chen et al., 2016; Kong et al., 2012; Sun et al., 2016; Zekri and Parsons, 1990). Additionally, plants accumulate compatible solutes, such as proline (Pro), glycine betaine, soluble sugars, and amino-acids or other compounds, under salt stress in order to reduce injury resulting from salinity stress (Hannachi and Van Labeke, 2018). Osmotic adjustment by compartmentalizing the inorganic ions in the vacuole also occurs (Kronzucker and Britto, 2011; Kronzucker et al., 2013).

Another adverse effect of salt stress is ion toxicity (Kronzucker et al., 2013; Munns and Tester, 2008). High Na^+ concentrations reduce plant photosynthesis (Wu et al., 2017) and compete with other nutrients, resulting in an intracellular ion imbalance (Hannachi and Van Labeke, 2018; Wang et al., 2017b). Therefore, controlling Na^+ uptake, and reducing the accumulation of Na^+ in the shoots, Na^+ recirculation to the roots, and Na^+ efflux to the external environment are important for improving salt tolerance in plants (Liang et al., 2018; Zhang et al., 2010; Zhang and Shi, 2013). Studies on non-uniform salinity in *A. nummularia* and alfalfa have indicated that leaf Na^+ is well regulated and remains in a lower range compared with uniform salinity (Bazihizina et al., 2009; Sun et al., 2016). Similar findings were reported in cotton by grafting using a split-root system, wherein decreased leaf Na^+ concentrations were considered to be associated with the transportation of excessive leaf Na^+ to the region of low salinity, as well as improved Na^+ efflux from the low salinity roots (Kong et al., 2012). Further studies are required to ascertain whether this Na^+ recirculation and Na^+ efflux is also present in plants that have not been grafted in this manner, as well as in additional species (Bazihizina et al., 2012).

Furthermore, salt stress induces nutritional disorders, especially potassium cations (K^+), which will affect important physiological metabolic processes that rely on K^+ , thereby inhibiting plant growth and development (Kiani et al., 2017; Munns and Tester, 2008). Under non-uniform salinity, increased leaf Na^+ concentrations are generally associated with declines in leaf K^+ concentrations in comparison with control treatments, though the leaf K^+ concentration still remains significantly higher than in plants under uniform salt stress (Bazihizina et al., 2009; Hamed et al., 2008). Cytoplasmic K^+ concentration may contribute towards salt tolerance (Chakraborty et al., 2016), and adequate root growth and function is dependent on adequate K^+ allocation (Wang et al., 2013). A reduction in K^+ loss from the roots in the high salinity parts may be necessary for facilitating growth in a non-uniform salinity environment in alfalfa (Sun et al., 2016).

Osmotic stress and ion toxicity can also cause oxidative stress and a series of secondary stresses (Liang et al., 2018), as well as generate excess reactive oxygen species (ROS) that cause cytoplasmic membrane damage and irreversible metabolic dysfunction (Kiani et al., 2017; Wang et al., 2017a). Antioxidant enzymes, including catalase (CAT, EC 1.11.1.6), peroxidase (POD, EC 1.11.1.7), superoxide dismutase (SOD, EC 1.15.1.1), and ascorbate peroxidase (APX, EC 1.11.1.11), are essential constituents of the ROS scavenging system that mitigate oxidative damage (Parida et al., 2004; Wang et al., 2016b). The significant role of antioxidant enzymes during the establishment of alfalfa seedlings under saline conditions was detailed in a previous study (Wang et al., 2009). Kiani et al. (2017) discovered that the CAT and POD activities of a barley mutant increased under salt stress, and this activity coincided with reduced levels of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in comparison to the wild-type. Except for the metabolic regulation of the shoots, the roots are directly in contact with saline soil and play important roles in enhancing salt tolerance, especially under non-uniform salinity (Bazihizina et al., 2012; Redwan

et al., 2017). The response and regulatory mechanisms of the root system on the low-saline side and high-saline side may be a localized or systemic response.

Alfalfa is one of the most economically important forage crops that is cultivated worldwide and valued for its high protein content. Although alfalfa is able to tolerate a moderate saline-alkaline environment, exposure to ~ 200 mM NaCl stress is associated with significantly reduced growth and productivity (Li and Brummer, 2012). Studying the response of alfalfa to non-uniform salinity would be an important contribution to our understanding of plant physiology under uniform salinity, and will also inform cultivation and management of agricultural fields with elevated salt concentrations. Additionally, as the salt-tolerance mechanism of the plant provides the theoretical basis from which to cultivate transgenic resistant varieties, an understanding of these mechanisms will inform the development of salt-tolerant cultivars.

In this study, the response of two alfalfa cultivars: “Zhongmu No.1”, a salt-tolerant cultivar, and “Algonquin”, a salt-sensitive cultivar, was evaluated when grown under uniform and non-uniform salt stress using a split-root system. The main objectives of our study were (i) to evaluate the effects of non-uniform salt stress on the growth of two alfalfa cultivars, (ii) evaluate the Na^+ and K^+ regulatory mechanisms of the leaves and roots under non-uniform salinity, and (iii) assess the antioxidant defense mechanisms in the leaves and both sides of the roots under non-uniform salt stress.

2. Materials and methods

2.1. Plant culture and the split-root system

We previously conducted a preliminary experiment to evaluate salt tolerance of six alfalfa varieties under uniform and non-uniform salt treatments. Based on results from this preliminary study, we selected two alfalfa cultivars, Zhongmu No.1 (salt tolerant) and Algonquin (salt sensitive), as these cultivars varied widely in salt-tolerance. Both cultivars' seeds were sterilized with 75% ethyl alcohol for 30 s and 5% sodium hypochlorite solution for 15 min, and then washed with distilled water 4–5 times. The seeds were sown (~ 1 cm depth) in plastic boxes containing sterilized wet sand and germinated for 7 d, at which point they reached the cotyledon stage with 4–5 cm long taproots. Seedlings exhibiting uniform growth were carefully selected and washed with distilled water. Surgical scissors were used to remove the root tips (5 mm) in order to encourage lateral root growth. The roots were then enclosed in sponge and placed in a plastic box and treated with three nutrient solution regimes: 0.1-strength nutrient solution for 4 d, followed by 0.5-strength solution for 7 d, and full-strength solution thereafter for 4 d. The full-strength nutrient solution consisted of the following: 2.5 mM $\text{Ca}(\text{NO}_3)_2$, 2.5 mM KNO_3 , 1 mM MgSO_4 , 0.5 mM $(\text{NH}_4)_2\text{H}_2\text{PO}_4$, 0.1 mM EDTA-FeNa, 0.2 μM CuSO_4 , 1 μM ZnSO_4 , 20 μM H_3BO_3 , 0.005 μM $(\text{NH}_4)_6\text{Mo}_{27}\text{O}_4$ and 1 μM MnSO_4 , adjusted to pH 6.5 with KOH. Split-root systems were established with these seedlings, as described in Sun et al. (2016). The split-root system consisted of two 0.35 L plastic cups and a foam board with a hole in the center. The healthy and uniform seedlings were selected and fixed on the foam board through the hole. The roots were separated into two approximately equal parts and divided into two plastic cups so the root system could be treated with different salt concentrations. All plants were placed in an artificial climate chamber with an average humidity of approximately 55%/90% day/night under a 16/8 h 25/20 °C light/dark regime.

2.2. Salt stress treatment

The seedlings were cultured in the split-root system for 5 d, at which time roots of the two different parts were treated with different NaCl concentrations. The experiment consisted of five treatments with 20

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