Scientia Horticulturae 245 (2019) 154–162

Contents lists available at ScienceDirect

Scientia Horticulturae

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

Comparative physiological responses and adaptive strategies of apple *Malus halliana* to salt, alkali and saline-alkali stress

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ARTICLE INFO

Keywords:
Malus halliana
Saline-alkali resistance
Photosynthesis
Chl fluorescence
Thermal dissipation
Osmotic regulation

ABSTRACT

Malus halliana Koehne (*M. halliana*) is a native rootstocks to the saline-alkali soil of Northwest China which shows a higher saline-alkali tolerance than other apple rootstocks. However, there are few studies of saline-alkali resistance on *M. halliana*. This study was aimed to elucidated the physiological adaptive mechanisms of *M. halliana* involved in the responce to three different stress factors. The salt stress (SS), alkali stress (AS) and saline–alkali stress (MAS) were applied to study the different responses of ion, photosynthesis, Chl fluorescence, antioxidant enzymes and osmolytes for 40 days. The results showed that *M. halliana* accumulated more Na^+ in roots and less K^+ in leaves under AS compared to the SS and MAS treatments. *M. halliana* plants adapted to three stresses by decreasing leaf water content (WC), stomatal conductance (G_s) and intercellular CO_2 concentration (C_i), increasing water use efficiency (WUE) and accumulating osmolytes. However, the respond mechanisms of *M. halliana* to SS, AS and MAS were different. Under SS, *M. halliana* plants adapted to stress by improving the activity of superoxide dismutase (SOD) and peroxidase (POD) and starting thermal dissipation protection mechanism. Under AS, plants mianly accumulated the organic acids (OA) to adjust osmotic balance and triggered xanthophyll cycle to dissipate excess energy. Under MAS, plants kept the dynamic balance of photosynthetic system between injury and repair by starting heat dissipation mechanism and xanthophyll cycle. And it also mianly accumulated osmolytes to maintain osmotic regulation and improved the activity of antioxidant enzyme to avoid oxidative damage. In addition, the analysis of principal component found that G_s, C_i, WC, Chl a + b (Chlorophyll), F_m (maximum fluorescence), F_v/F_m (maximal photochemical efficiency), ETR(photosynthetic electron transport rate), ΦPSII (actual photochemical efficiency) and qP (photochemical quenching coefficient) were major influencing factors to the decreasing of P_n (net photosynthetic rate). In summary, the inhibitory effects of growth and photosynthesis on *M. halliana* under three stresses were AS > MAS > SS. Under MAS, the salt and alkail had a certain synergistic effect.

1. Introduction

Apple (*Malus pumila* Mill.) is one of the most important fruit tree that is cultivated widely throughout the world (Musacchi and Serra, 2018). The northwest China is the optimal ecological area for growing apples, having more than 70% of the agricultural area with mixed NaCl and $NaHCO_3$ high-pH soil (Kawanabe and Zhu, 1991). The saline/alkali reaction of soil is a key limiting factor for apple growth and productivity (Alizadeh et al., 2013). The rootstock can affect plant growth, fruit yield and quality (Sabatino et al., 2018). In apple industries, the rootstocks with excellent tolerance have been widely applied to improve the resistance of plant (Sau et al., 2018). Therefore, it is important to study the rootstock resources of high resistance for the development of apple industry in saline-alkali soil (Wang et al., 2018a,b,c).

Numerous studies have suggested that salt and alkali stress are two distinct types of stress for plants. Salt stress generally involves osmotic stress, ion injury and oxidative stress (Wei et al., 2017). Osmotic imbalance causes water deficit, reduced leaf area expansion and stomatal closure which ultimately lessen the photosynthesis and inhibit growth of plants (Roy et al., 2014). The ionic stress causes the excess accumulation of Na^+ in the leaves which lead to premature senescence in older leaves and production of reactive oxygen species (ROS) (Munns and Tester, 2008). However, under alkali stress, the reactions of plants

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https://doi.org/10.1016/j.scienta.2018.10.017
Received 13 July 2018; Received in revised form 6 October 2018; Accepted 9 October 2018
0304-4238/ © 2018 Published by Elsevier B.V.

are consistent with the ones under salt stress in addition of the influence of high-pH level. High pH may inhibit ion uptake and plants can not sufficiently absorb metal ions ($Mg^{2+}$and Fe^{2+}) needed to synthesize Chl (Guo et al., 2015). It may also damaged photosynthetic organ, weakened the capture of light energy by PSII and inhibited photosynthetic electron transport (Gerloff-Elias et al., 2010).

It has been reported that photosynthetic capacity of plant usually is inhibited under salt stress (Lacerda et al., 2003). Generally, the reduction of P_n (net photosynthetic rate) is mainly result from stomata and non stomatal factors. G_s (stomatal conductance) is main stomata factor to the decreasing of P_n, which G_s often closely correlated with the change of water potential (Liu and Shi, 2010). It is considered that plants can lose water as a quick and economical approach to osmotic adjustment in response to salt stress conditions (Yang et al., 2010). Romera et al. (2014) reported that salinity can lead to cell membrane dehydration, which plants can reduce loss of water from the leaves by closing stomata. Moreover, the conversion of photochemical energy under salt and alkail stress was inhibited. Thus, excess light energy can not be utilized through the photosynthetic electron transport pathway, which reduce the photosynthetic efficiency (Zuo et al., 2014). The thermal disspation and xanthophyll cycle have been thought to be a protection mechanism that dispatcher excess light energy (Guo et al., 2009).

Plants subjected to salt and alkali stress are likely to experience serious water shortages, which could easily lead to oxidative damage (Maeda et al., 2011). Osmotic stress leads to the formation of reactive oxygen species. To scavenge the ROS, the activities of antioxidative enzymes, such as superoxide dismutase (SOD), guiacol peroxidase (POD), increase. Osmotic adjustment of plant is another defense strategy against salt and alkali stress. Plants could enhance their resistance to the osmotic stress by the accumulation of osmolytes under salt stress (Chen et al., 2011). For example, the accumulation of proline, sugars and OA which play positive roles in plant's regulation of cell osmotic pressure, pH balance and ROS removal (Song et al., 2017). Some reports have clearly demonstrated that proline can reduce the levels of reactive oxygene species (ROS) generated during osmotic stress and directly impact on intracellular K^+/Na^+ homeostasis (Pang et al., 2007). In recent years, most of the research studied the mechanisms on saline-alkail tolerance have emphasized on SS and AS with a little focused on MAS. However, these reports have focused on the effects of MAS on gramineous plants (wheat, maize) and studies on apple rootstocks have been rarely performed.

M. halliana is an endemic apple rootstock with excellent resistance, which originated from Hexi Corridor of Gansu province. It has been reported that *M. halliana* have higher drought resistance and iron deficiency resistance than other apple rootstocks by our subject (Wang et al., 2018a,b,c), and we have found that *M. halliana* grows well in saline-alkali soil. Thus, understanding the mechanism of saline-alkali tolerance of *M.halliana* may provide guidance for breeding apple rootstock. However, there are few studies of aline-alkali resistance on *M. halliana*. In this paper, the two-year-old seedings of *M. halliana* were employed as experimental materials and three types of stress treatments, (i) salt stress (NaCl) (SS), (ii) alkali stress ($NaHCO_3$) (AS) and (iii) saline-alkaline stress (1:1 M ratio of NaCl : $NaHCO_3$) (MAS), were simulated by watering Hogland nutrient solution. The aim of this study was to examine the effects of three stresses treatments on the leaf phenotype, ion balance (Na^+ and K^+ in leaves, stems and roots), photosynthesis, pigment contents, Chl fluorescence and physiology (antioxidant system, solute accumulation) of *M. halliana*. Furthermore, the different physiological adaptive mechanism of plants under SS, AS and MAS were compared.

2. Materials and methods

2.1. Plant materials

Two-year-old of *M. halliana* seedlings were collected from nursery located in Jingyuan, Gansu Province, Northwest China. The experiment was performed in greenhouse of Gansu Agricultural University (Gansu Province, China) in April 2017. Plants were transplanted in pottery basin pots with a diameter of 25 cm containing 3.5 kg of nutrient matrix (the volume ratio of vermiculite, perlite and peat is 1:1:3). Each pot contained one plant. The pots were well drained with holes at the bottom.

2.2. Experimental design

Stress treatments were conducted on May 20, 2017. Fourty uniform (the height of each plant was 80 cm) and healthy plants were individually potted and randomly divided into 4 sets. One set was used as control, and the remaining 3 sets were used for three stress treatments. Each treatment was repeated ten times.

2.3. Stress treatments

Experiment included four groups, namely: control (CK), salt stress (NaCl) (SS), alkali stress (NaHCO3) (AS) and mixed saline-alkaline stress (1:1 M ratio of NaCl : NaHCO3) (MSA). According to previous results, we screened the 100 mM to carry the experiment. The salt composition of the three treatments was listed in Table 1. The control groups were watered with only 500 mL Hoagland and stress groups were watered with 500 mL Hoagland solution containing the corresponding salts, all groups were treated around 17:00–18:00 every three day. The Hoagland solution was consisted of macroelement (KNO_3, NH_4NO_3, KH_2PO_4, $MgSO_4$), calcium salt ($Ca(NO_3)_2{\cdot}4H_2O$), microelement (KI, H_3BO_3, $MnSO_4$, $ZnSO_4$, Na_2MoO_4, $CuSO_4$, $CoCl_2$) and ferris salt ($FeSO_4{\cdot}7H_2O$, EDTA·Na). At beginning of the stress, to avoid salt shock reaction, an increase of 50 mM treatment concentrations per day was applied and the treatment period was recorded after reaching the final concentration, respectively. All parameters were measured after 40 days of treatment.

2.4. Measurement of indices

The functional leaves were digested with HNO_3 by microwave digestion. Na^+ and K^+ contents was determined by Flame spectrophotometer method (TAS-990, Purkinje General, Beijing, China). Leaf water content (WC) was calculated using the formula (FW-DW) × 100/FW (FW, fresh weigh; DW, dry weigh) and expressed as a percentage (Yang et al., 2008a,b). Electrolyte leakage (EL) was determined by DDS-307 conductivity (LeiCi, Shanghai, China), the formula as follows: EL (%) = (EL1–EL0)/(EL2–EL0) × 100%. To do this, the collected leaves

Table 1
Concentrations (mM) of various salts (NaCl, $NaHCO_3$) in treatments.

Treatment	NaCl (mM)	$NaHCO_3$ (mM)	Salinity(mM)	pH
CK	0	0	0	6.80
SS	100	0	100	7.00
AS	0	100	100	9.00
MAS	50	50	100	8.20

CK, control; SS, salt stress (NaCl) ; AS, alkali stress ($NaHCO_3$); MSA, mixed saline-alkaline.
stress (1:1 M ratio of NaCl : $NaHCO_3$). The same as below.

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