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Balance between salt stress and endogenous hormones influence dry matter accumulation in Jerusalem artichoke

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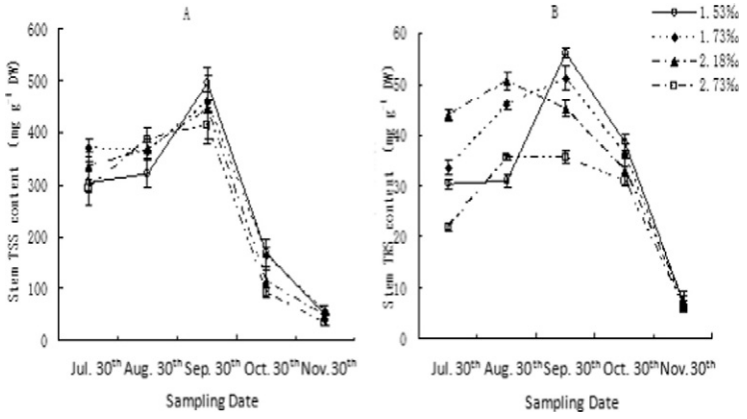
HIGHLIGHTS

- Production of Jerusalem artichoke on saline land is strategically important for using saline land resources
- Endogenous hormones [zeatin (ZT), auxins (IAA), gibberellins (GA_3) and abscisic acid (ABA)] in regulating sugar and dry matter accumulation in tubers was characterized for the first time
- Tuber yield would significantly decreased with the increase of salinity

GRAPHICAL ABSTRACT



Effect of soil salinity on concentration of total soluble sugars (TSS, A) and total reducing sugars (TRS, B) in stems of Jerusalem artichoke.

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ABSTRACT

Salinity is one of the most serious environmental stresses limiting agricultural production. Production of Jerusalem artichoke on saline land is strategically important for using saline land resources. The interaction between plant hormones and salinity stress in governing Jerusalem artichoke (*Helianthus tuberosus*) growth is unclear. Jerusalem artichoke (variety Nanyu-1) was grown under variable salinity stress in the field, and a role of endogenous hormones [zeatin (ZT), auxins (IAA), gibberellins (GA_3) and abscisic acid (ABA)] in regulating sugar and dry matter accumulation in tubers was characterized. Under mild salt stress (≤2.2 g NaCl kg^{-1} soil), Nanyu-1 grew well with no significant alteration of dry matter distribution to stems and tubers. In contrast, under moderate salt stress (2.7 g NaCl kg^{-1} soil), the distribution to stem decreased and to tubers decreased significantly. Mild salt stress induced sugar accumulation in tubers at the beginning of the tuber-expansion period, but significantly inhibited (i) transfer of non-reducing sugars to tubers, and (ii) polymerization and accumulation of fructan during the tuber-expansion stage. Under different salinity stress, before the stolon growth, the ratio of IAA/ABA in leaves increased significantly and that of GA_3/ABA increased slightly; during tuber development, these ratios continued to decrease and reached the minimum late in the tuber-expansion period. While, salt stress inhibited (i)

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underground dry matter accumulation, (ii) tuber dry matter accumulation efficiency, (iii) transport of non-reducing sugars to tubers, and (iv) fructan accumulation efficiency during the tuber-expansion period; these effects were accompanied by significantly decreased tuber yield with an increase in salinity. With soil salinity increasing, the synthesis of IAA and GA_3 was inhibited in leaves and tubers, while ABA synthesis was stimulated. In brief, tuber yield would significantly decreased with the increase of salinity.

1. Introduction

Saline-alkali soils are distributed widely around the world (around 954 million hectares, representing 10% of the total arable land), making them one of the most important land resources (Liu et al., 1998). China has 99 million hectares of saline-alkali soils, accounting for about 25% of arable land (Liu et al., 1998). A proportion of these soils is distributed in the coastal zone (approximately 2.1 million hectares of saline-alkali soils, increasing at a rate of about 20–30,000 ha annually).

Soil salinity decreases the soil resource value, causes huge losses to the production agriculture and poses a threat to the environment, thus representing the economic and environmental hazards (Long et al., 2014). The degree of soil salinization in China is generally high, making it difficult for crops to survive. Given a relatively small amount of arable land per capita in China, the effective utilization of saline soil can result in a good combination of economic benefits, environmental protection and sustainable development, underpinning its practical significance (Long et al., 2014).

Jerusalem artichoke (*Helianthus tuberosus*), family Asteraceae, is a hardy plant with high photosynthetic efficiency, low fertilizer demand, powerful ecological restoration features (used in terracing and in loose sand) and high value arising from a wide range of uses. Its tolerance to many abiotic stresses (including salinity and alkalinity), strong reproductive capacity and broad adaptability make Jerusalem artichoke an ideal plant species for improving saline-alkali soils (Ma et al., 2011; Long et al., 2016).

Studies showed that Jerusalem artichoke variety Nanyu-1 produced higher tuber yield and had higher fructan content under moderate salt stress than other varieties, and therefore can be used as a non-food energy plant to improve and utilize saline land (Jin et al., 2013; Gunnarsson et al., 2014; Baldini et al., 2004). Currently, there is no systematic knowledge of the physiological processes governing salt tolerance of Jerusalem artichoke tubers (Long et al., 2009). Soluble sugars as osmotic substances are considered important for Jerusalem artichoke resistance to salt stress. Jerusalem artichoke tuber yield is closely related to the fructan metabolism, and key enzymes in the synthesis of soluble sugars are induced by salt and ABA (Jiménez-Bremont et al., 2007). We speculated that endogenous plant hormones were involved in regulating tuber development under salt stress in Jerusalem artichoke.

In this paper, we characterized (i) dry matter accumulation and sugar biosynthesis, translocation and partitioning, and (ii) dynamics in endogenous hormone concentrations and tuber formation and development in Jerusalem artichoke under salt stress.

2. Materials and methods

2.1. Plant and soil material

Jerusalem artichoke variety Nanyu-1 (*H. tuberosus* L. cv. NY-1) was used in the study. We selected Nanyu-1 from four different soil salinity habitats that naturally exist at Jinhai farm of Dafeng City (32°59′N, 120° 49′E). The soil had the following average properties: pH 7.45–8.15 (Jenway 3540, Bibby Scientific Limited, UK) (Jiang et al., 2015). Organic carbon 33.42 g kg^{-1}, total nitrogen 4.15 g kg^{-1}, total phosphorus 2.72 g kg^{-1}, total potassium 26.63 g kg^{-1}, available phosphorus 17.48 mg kg^{-1}, available potassium 124.35 mg kg^{-1}. Soil samples were taken randomly at five points in an "S" pattern in each replicate plot using a soil auger (6 cm diameter) at 0–20 cm depths (Edward et al., 2015). Each sample was set three biological replicates. Soil samples were packed in individual sterile kraft bags (Chenery et al., 2012), and transferred on ice to the laboratory. Each soil sample was air-dried, passed through a 0.25-mm sieve, and stored at room temperature for analyses. The total salt content at four different sites was: 1.5, 1.7, 2.2 and 2.7 g NaCl kg^{-1}. The first three soils were categorized as mildly saline (1.0–2.5 g kg^{-1}), and the final group was moderately saline (2.5–4.0 g kg^{-1}) (Wang, 1993). The soil was ploughed in winter using a conventional mould board plough and was then tilled twice more prior to sowing tubers. Plot size was 5 m in length and 4 m in width with three replicates. The Jerusalem artichoke (cv Nanyu No. 1) was planted in March. Plant row spacing was 60 cm inter-row, and intra-row distance between plants was 40 cm.

2.2. Dry matter accumulation and distribution

Six replicate plant samples were taken in each plot during tuber development at the following growth stages: seedling stage - July 30; tuber formation - August 30; early stage of tuber expansion - September 30; middle stage of tuber expansion - October 30; and late tuber expansion - November 30 (Aksenova et al., 2012). At each sampling, the whole plant of Jerusalem artichoke was excavated, and youngest fully-expanded leaves and stolons or tubers were washed in deionized water, blotted dry with absorbent paper, wrapped in foil, placed in separate 50-mL centrifuge tubes, and snap-frozen in liquid nitrogen for transport to the lab. The samples were stored at −70 °C. The rest of the plant was separated into leaves, stems, roots and tubers, dried at 105 °C for 15 min and then at 75 °C until constant weight.

2.3. Sugar accumulation and distribution

Dried plant material was ground to a powder and passed through an 80-mesh sieve. Soluble sugars were extracted from 0.5-g sample in 10 mL of deionized water at 90 °C in a water bath for 50 min; cooled the samples and then through four layers of filter cloth and collect the filtrate, and the residue was re-extracted twice in the same way. The supernatants were combined into a 100-mL volumetric flask, 10 mg of activated carbon was added, and discoloration proceeded at 80 °C for 30 min followed by filtration. Soluble sugars in the filtrate were determined using the sulfuric acid method. Absorbance was measured at 490 nm against the fructose standard.

Liquid chromatography with an evaporative luminescence detector was used for determination of fructan and soluble sugar concentrations: let 1 mL extract of soluble sugars through 0.45 nm organic membrane, then tested use the equipment. The conditions were: column temperature 30 °C, injection volume 10 μL, gradient elution: 0–15 min: water 25%: 75% acetonitrile; 15–30 min: water 35%: 65% acetonitrile; 30–40 min: water 45%, 55% acetonitrile; 40–42 min: water 50%, 50% acetonitrile; 42–55 min: water 25%, 75% acetonitrile (all % are v/v) (Li et al., 2014).

Tuber fructan accumulation (g $plant^{-1}$) = (C × W)/1000

Tuber fructan accumulation rate (mg $plant^{-1}$ d^{-1}) = ($M_t - M_0$)/DC, fructan concentration in tubers (mg g^{-1} DW); W, tuber dry weight (g), M_t, fructan content (g) in tubers at the current sampling (g); M_0,