Environmental and Experimental Botany 99 (2014) 86–99

Contents lists available at ScienceDirect

Environmental and Experimental Botany

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

Responses of nutrient dynamics in barley seedlings to the interaction of salinity and carbon dioxide enrichment

Usue Pérez-López*, Jon Miranda-Apodaca, Amaia Mena-Petite, Alberto Muñoz-Rueda

Departamento de Biología Vegetal y Ecología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, UPV/EHU, Apdo. 644, E-48080 Bilbao, Spain

ARTICLE INFO

Article history:
Received 30 July 2013
Received in revised form
18 September 2013
Accepted 5 November 2013

Keywords:
Climate change
Elevated CO_2
Hordeum vulgare
Mineral nutrition
Salinity

ABSTRACT

The effects of elevated CO_2 on the content of several nutrients in plants have been well studied, but few studies have investigated plant nutrient dynamics under future environmental conditions, which are expected to include elevated CO_2 and elevated soil salt concentrations. This study investigated whether high salt and CO_2 conditions, singly or in combination, might affect nutrient dynamics, and the underlying mechanisms. We measured macro- and micronutrient uptake and translocation rates, nutrient content and concentrations in whole seedlings and in each plant organ. We estimated whole-plant nutrient use efficiencies in barley subjected to 0, 80, 160, or 240 mM NaCl and grown at either 350 (ambient) or 700 (elevated) $\mu mol\ mol^{-1}$ CO_2. Under non-saline conditions, plants grown at elevated CO_2 adjusted their root size and activity to change nutrient uptake and transport efficiency in response to the demand for a given nutrient. Under high saline conditions, salt stress reduced K, Ca, N, B, and S uptake rates and concentrations in tissues, which caused growth reduction. Nevertheless, barley had the ability to increase the selectivity of K over Na, and Ca over Na. Under combined conditions of salt stress and elevated CO_2, barley seedlings were able to maintain higher uptake and translocation rates of almost all nutrients. This ability allowed the plants to adapt to higher demands under elevated CO_2; they could grow more rapidly by allocating more C to root growth and by increasing active nutrient uptake and translocation. Our results indicated that salinity generally increased nutrient use efficiency under both CO_2 conditions. However, we found no consistent evidence that nutrient use efficiency was affected by CO_2 concentration, either under non-saline or saline conditions.

1. Introduction

It has been predicted that, by the end of this century, atmospheric carbon dioxide concentration will amount to 700 $\mu mol\ mol^{-1}$ (IPCC, 2007). Numerous controlled-environment studies suggest that the global increase in atmospheric CO_2 will have significant positive effects on plant photosynthetic rates, growth, and production. Those effects depend on conditions where other resources are not limiting (Kimball, 1983), because plants must be well-supplied with nutrients and water to make a full use of the elevated CO_2 concentrations. Thus, during CO_2 enrichment, an increased carbon supply is typically co-ordinated with a change in the demand for other nutrients (Rogers et al., 1999). However, results vary, perhaps reflecting the great diversity of experimental procedures used in those studies (e.g., different plant species and nutritional levels were employed). For instance, plants grown in high CO_2 with soil nutrients ranging from adequate to deficient often exhibit reduced tissue nutrient concentrations; in contrast, under high soil nutrient conditions, tissue nutrient concentrations are not affected by applied CO_2 (Prior et al., 1998 and literature therein; Zhang and Dang, 2006; Shinano et al., 2007).

Current reviews of the literature suggest that, with CO_2-enrichment, whole plant nutrient content is often increased, but tissue nutrient concentration is reduced (Rogers et al., 1994; Prior et al., 1998; Duval et al., 2012; McGrath and Lobell, 2013). Currently, we possess only a limited understanding of the mechanisms involved in this phenomenon. Many biological and physical processes are potentially affected by growth in elevated CO_2 conditions, due to (1) nutrient dilution by enhanced carbohydrate accumulation; (2) alterations in physiological requirements, which change the uptake rate and the partitioning of nutrients among organs; (3) reduction of the transpiration rate with a consequent decrease of nutrient flow to the roots; (4) changes in nutrient use efficiencies; (5) increases in the volume of soil that can be explored by the roots; and/or (6) increases in the active root uptake rates (Rogers et al., 1994; BassiriRad et al., 1996; Chen et al., 1997; Fangmeier et al., 2002; Taub and Wang, 2008; McGrath and Lobell, 2013). Moreover, the afore mentioned mechanisms

Abbreviations: XTR, nutrient translocation rate; XUE, nutrient use efficiency; XUR, nutrient uptake rate.

* Corresponding author. Tel.: +34 94 601 3374; fax: +34 94 601 35 00.
E-mail address: usue.perez@ehu.es (U. Pérez-López).

0098-8472/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.envexpbot.2013.11.004

could be modified by other factors, such as drought and/or salinity.

According to recent statistics (FAO, 2000), salinity currently affects 19.5% of the world's irrigated area, and it also occurs on non-irrigated croplands and rangelands. Moreover, salinity-affected areas are rapidly increasing, due to faulty irrigation systems and poor water quality. Salinity in the soil is a major stressor and, particularly in arid and semi-arid regions, it can severely limit crop production. The mechanisms that plants have evolved for nutrient uptake, transport, recirculation, and utilisation may not function optimally under saline conditions (Lazof and Bernstein, 1999; Cramer, 2002; Munns et al., 2006). Under saline conditions, soil Na and Cl concentrations may exceed the concentrations of essential macronutrients by an order of magnitude, and they may exceed the concentrations of micronutrients to even a greater extent. The resulting changes in ion activities in the soil solution and changes in the ratios of Na to specific macronutrients, like Ca and K, may induce changes in nutrients root uptake activity and their translocation within the plant. As a result, macro- and micronutrient concentrations in plant tissues often change under increased salinity; thus, plants may become susceptible to specific ion injuries and nutritional disorders (Ashraf, 1994; Marschner, 1995; Niu et al., 1995; Munns, 2005; Parida and Das, 2005).

Among the cereals, barley is one of the most tolerant to salinity. Under saline conditions, barley has the ability (1) to perform osmotic adjustments by compartmentalizing toxic salt ions in cell vacuoles, which preserves a favourable K/Na ratio in the cytoplasm at high leaf Na concentrations; (2) to induce Ca transport to the shoot; (3) to differentially distribute ions between epidermal and mesophyll cells; and (4) to induce antioxidant metabolism (Fricke et al., 1996; Munns et al., 2006; Pérez-López et al., 2009b, 2010b) among other activities. Nevertheless, salinity reduces barley growth when concentrations are higher than 8 dSm^{-1}, due to alterations in water and nutrient uptake rates and decreases in photosynthesis (Pérez-López et al., 2010a, 2012, 2013a, 2013b). However, although much effort has been dedicated to correlating these changes to the degree of salt tolerance in a plant, no agreement has been reached among studies (Chen et al., 2007; Genc et al., 2007). Moreover, the relevance of plant salt tolerance mechanisms may change in future environmental conditions, where increasing saline areas will be combined with increases in atmospheric CO_2 concentrations. In view of the fact that salinity decreases the concentrations of some essential nutrients (Ca and K, among others) and increases the concentrations of others (Na and Cl), and that elevated CO_2 also decreases or enhances these nutrient concentrations, it seems logical to study how plants would respond to combinations of saline and CO_2 conditions.

Several authors have shown that, in response to salt and elevated CO_2 treatments, plant nutrient concentrations varied dramatically between species. For example, in *Olea europaea* cv. Koroneiki (Melgar et al., 2008) and citrus rootstocks (García-Sánchez and Syvertsen, 2006), differences in mineral content have been detected under different CO_2 concentrations. However, in other species, such as *Aster tripolium* (Geissler et al., 2009), *Spartina densiflora* (Mateos-Naranjo et al., 2010), and *O. europaea* cv. Picual (Melgar et al., 2008), salinity and CO_2 enrichments did not appear to interact with either Na or Cl absolute levels. Despite this variability, no reports have evaluated the interactive effects of CO_2 and salinity on nutrient acquisition, partitioning, and use efficiencies. Therefore, we lack an integrated picture of how environmental changes might affect these processes. This lack has prompted us to propose three objectives for the present study: (1) to determine whether salt treatments and CO_2 conditions, singly or in combination, would affect nutrient content in whole plants and in individual plant organs; (2) to determine the effects of salinity on nutrient uptake and translocation rates and the mechanisms by which elevated CO_2 concentration affects these processes; and (3) to evaluate whether barley growth is impacted by salt-induced alterations in different nutrient concentrations, to determine whether elevated CO_2 concentration might alleviate those effects, and if so, to investigate the underlying mechanism. To achieve these objectives, we measured nutrient uptake and translocation rates, nutrient contents, and nutrient concentrations in whole plants and in individual plant organs. We also measured whole-plant nutrient use efficiency and nutrient selectivity in barley seedlings grown under non-saline (0 mM NaCl) and saline (80, 160, and 240 mM NaCl) conditions at ambient (350 $\mu mol\ mol^{-1}$) or elevated (700 $\mu mol\ mol^{-1}$) CO_2 concentrations.

2. Materials and methods

2.1. Plant materials, growth conditions, and treatments

Six barley (*Hordeum vulgare* L. cv. Iranis) seeds per pot, equivalent to 2.6 $g\ m^{-2}$, were sown in 2500 cm^3 plastic pots filled with a medium consisting of a mixture of perlite/vermiculite (3/1, v/v). Plants were grown in CO_2-controlled growth chambers (Conviron E15; Conviron, Manitoba, Canada). The chambers were maintained 24 h per day at a CO_2 concentration of 350 $\mu mol\ mol^{-1}$ (ambient) or 700 $\mu mol\ mol^{-1}$ (elevated). The plants were grown under a 14-h photoperiod with 400 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic active radiation provided by a combination of incandescent bulbs and warm-white fluorescent lamps (Sylvania F48T12SHO/VHO, Sylvania, USA). The relative day/night humidity was 70/80%, and the day/night temperature was 24/20 °C. To minimize the effects of intra-chamber environmental gradients, the plants were randomly repositioned within the chamber each week (Hymus et al., 2001). The plants were watered with Hoagland's solution (Arnon and Hoagland, 1940) every two days, until the first leaf had completely expanded (14 days). After that, from days 14 to 28, seedlings were watered every two days with 250 mL of Hoagland's solution supplemented with increasing concentrations of NaCl: 0 mM (2.0 $dS\ m^{-1}$), 80 mM (9.7 $dS\ m^{-1}$), 160 mM (17.6 $dS\ m^{-1}$), or 240 mM (24.4 $dS\ m^{-1}$) (Pérez-López et al., 2009a). At the beginning of the experimental period (day 14) and at the end of the experimental period (day 28), the seedlings were harvested and separated into leaves, stems, and roots.

2.2. Determination of nutrient concentrations in plant tissues

Inorganic ions (Na, Cl, K, Ca, Mg, P, S, B, Fe, Mn, Cu, and Zn) were extracted from dry matter that had been finely ground and digested with nitric acid (1%). The ion contents were quantified with inductively coupled plasma-optical emission spectrometry (Thermo Iris Advantage Ers Duo, USA). N was determined from finely ground dry matter, digested according to the Kjeldahl method (AOAC, 1990).

2.3. Determination of nutrient uptake and translocation rates

The nutrient uptake and translocation rates were calculated based on equations described by Franklin and Zwiazek (2004). The nutrient uptake rate was calculated as: $[(M_{tot2} - M_{tot1}) \times (\ln(W_{r2}/W_{r1}))]/[(T_2 - T_1) \times (W_{r2} - W_{r1})]$; where M_{tot} was the average content of nutrient per plant (mg) at the beginning (M_{tot1}) and end (M_{tot2}) of the salinity treatment; T_1 and T_2 were the beginning and ending days of the experiment, respectively; and W_r was the mean root dry weight (g) at the beginning (W_{r1}) and end (W_{r2}) of the salinity treatment. The nutrient translocation rate was calculated as: $[(M_{aer2} - M_{aer1}) \times (\ln(W_{r2}/W_{r1}))]/[(T_2 - T_1) \times (W_{r2} - W_{r1})]$; where M_{aer} was the average content of nutrient per aerial portion (mg) at the beginning (M_{aer1}) and end (M_{aer2}) of the salinity treatment.