



Carbon dioxide enrichment moderates salinity-induced effects on nitrogen acquisition and assimilation and their impact on growth in barley plants

Usue Pérez-López^{a,*}, Anabel Robredo^a, Jon Miranda-Apodaca^a, Maite Lacuesta^b, Alberto Muñoz-Rueda^a, Amaia Mena-Petite^a

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

^b Departamento de Biología Vegetal y Ecología, Facultad de Farmacia, Universidad del País Vasco, UPV/EHU, P^o de la Universidad 7, 01006 Vitoria-Gasteiz, Spain

ARTICLE INFO

Article history:

Received 19 April 2012

Received in revised form

28 September 2012

Accepted 24 October 2012

Keywords:

Climate change

Elevated CO₂

Hordeum vulgare

Nitrogen isotope discrimination

Nitrogen metabolism

Salt stress

ABSTRACT

Both salt stress and high carbon dioxide (CO₂) levels can affect plant nitrogen (N) metabolism by acting in parallel, decreasing N metabolism; or acting in opposite directions, with salt stress decreasing N metabolism and elevated CO₂ levels enhancing it. The objective of this work was to analyse the effect of salinity on N acquisition, distribution, and assimilation, the consequences of these effects on growth in barley (*Hordeum vulgare* L., cv. Iranis), and the possible effects on these processes provoked by elevated CO₂ levels. Several steps of N metabolism were studied in *H. vulgare* plants exposed to 0, 80, 160, or 240 mM NaCl under ambient (350 μmol mol⁻¹) or elevated (700 μmol mol⁻¹) CO₂. Salt stress reduced the N uptake (NUR) and translocation (NTR) rates and nitrate reductase (EC 1.7.1.1) activity, altering plant N isotope discrimination (Δ¹⁵N). Although salt stress increased glutamine synthetase (EC 6.3.1.2) activity, N and protein content, and photosynthetic nitrogen use efficiency decreased. The decrease in nitrate reductase activity was related to decreases in NUR and NTR, while Δ¹⁵N correlated with the NUR and with the nitrate reductase activity. Under mild salt stress, N metabolism was better maintained under elevated CO₂ levels than under ambient CO₂ levels, since NUR, NTR, photosynthetic nitrogen use efficiency, and nitrate reductase activity were less affected, yielding lower Δ¹⁵N and higher growth. In addition, growth was negatively correlated with Δ¹⁵N indicating that the Δ¹⁵N determination may allow the estimation of barley growth. As a consequence of all these results, barley plants subjected to elevated CO₂ levels will likely overcome mild saline conditions because of their capacity to maintain efficiency in N metabolism.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

The ability of plants to acquire and assimilate nitrogen (N) is an important determinant of plant growth. Inorganic N is generally taken up by higher plants as nitrate (NO₃⁻) and, to a lesser extent, as ammonium (NH₄⁺). Following uptake by NO₃⁻ transporters,

Abbreviations: A, photosynthetic rate; ATP, adenosine 5'-triphosphate; DW, dry weight; δ¹⁵N, nitrogen natural isotopic signature; Δ¹⁵N, nitrogen isotope discrimination; EDTA, ethylenediaminetetraacetic acid; GS, glutamine synthetase; NH₄⁺, ammonium; NiR, nitrite reductase; NO₃⁻, nitrate; NR, nitrate reductase; NR_{act}, actual nitrate reductase; NR_{max}, maximum nitrate reductase; NTR, nitrogen translocation rate; NUE, whole-plant nitrogen use efficiency; NUR, nitrogen uptake rate; PNC, plant nitrogen concentration; PNUE, photosynthetic nitrogen use efficiency; RGR, relative growth rate; RuBisCO, ribulose-1,5-bisphosphate carboxylase oxygenase.

* Corresponding author. Tel.: +34 94 601 3374; fax: +34 94 601 3500.

E-mail addresses: usue.perez@ehu.es (U. Pérez-López), anabel.robredo@ehu.es (A. Robredo), jon.miranda@ehu.es (J. Miranda-Apodaca), maite.lacuesta@ehu.es (M. Lacuesta), a.munoz-rueda@ehu.es (A. Muñoz-Rueda), amaia.mena@ehu.es (A. Mena-Petite).

NO₃⁻ is reduced in the cytosol by nitrate reductase (NR) to nitrite, which is in turn reduced to NH₄⁺ in the chloroplast by nitrite reductase (NiR). NH₄⁺ is assimilated by a concerted action of glutamine synthetase (GS) and glutamate synthase (GOGAT; Ireland and Lea, 1999). NO₃⁻ uptake, reduction to NH₄⁺ and its assimilation require energy and carbon skeletons provided by photosynthesis and tricarboxylic acid cycle. Thus, several of these steps are affected under stressful environmental conditions such as drought and/or salinity (Parida and Das, 2005; Debouba et al., 2006; Fresneau et al., 2007; Robredo et al., 2011).

Soil salinization is an important growth limiting factor for most plants (FAO, 2007). Around 20% of the irrigated lands and one-third of the world arable soil are affected by a progressive salinization. Salinity causes many changes in plant physiology, including alterations in water and nutrient uptake (Munns, 2005; Parida and Das, 2005), decreases in photosynthetic rates (A; Chaves et al., 2011), induction of oxidative stress (Dionisio-Sese and Tobita, 1998; Sgherri et al., 2007; Pérez-López et al., 2009b, 2010b) and alteration of N metabolism (Munns, 2005), which largely influences plant growth (Gouia et al., 1994). In non-halophytes, N uptake,

translocation, and assimilation as well as nitrogen natural isotopic signature ($\delta^{15}\text{N}$) appear to be especially sensitive to salinity (Mariotti et al., 1982; Kaiser and Förster, 1989; Gouia et al., 1994; Dubey and Pessaraki, 1995; Peuke and Jeschke, 1999; Abd-El Baki et al., 2000; Debouba et al., 2006). The osmotic effects induced by NaCl can initially disrupt root membrane integrity (Carvajal et al., 1999) and decrease photosynthetic and transpiration rates (Parida and Das, 2005). These responses could cause (1) restrictions in the loading of NO_3^- into the xylem due to a decrease in water absorption and/or an inhibition of NO_3^- transporters (provoked by a lack of adenosine 5'-triphosphate (ATP) and/or direct competition with Cl^-) and (2) reductions in NR and GS activities due to a lack of reducing power, carbon skeletons, and ATP provided by photosynthesis and the tricarboxylic acid cycle (Diaz et al., 1995, 1996). Consequently, salt-dependent N deficiencies may contribute to growth limitation. In addition to the osmotic effect, salt stress induces ionic effects, i.e. Cl^- and Na^+ may directly affect NO_3^- transporters, NR activity, and GS activity (Flores et al., 2000).

Together with the increase in surface area under salinization, it is anticipated that the concentration of CO_2 in the atmosphere will double by the end of the century (IPCC, 2007). As Stitt and Krapp (1999) stated, N is a key regulator of the plant response to elevated CO_2 levels; acquisition and reduction of NO_3^- and assimilation of NH_4^+ are important components of this response (Natali et al., 2009), although the changes in N metabolism in response to CO_2 enrichment are not thoroughly understood at the biochemical level. Previous studies have investigated the effects of elevated CO_2 levels on N metabolism, and improvement, depression, or no effects have been recorded. N and carbon assimilation compete for reductants (Bloom et al., 2002) that could depress N assimilation. Several investigations (Ferrario-Méry et al., 1997; Bloom et al., 2002) have indicated that, for a variety of species, NR activity is lower when plants are grown at elevated CO_2 levels compared to ambient levels. Lower transpiration rates may reduce the driving force for NO_3^- movement from the soil to the leaves (Chen et al., 1997; Fangmeier et al., 2002), decreasing NO_3^- availability for NR activity. However, it has been postulated that when there is no restriction of NO_3^- in the medium, N assimilation is higher in plants grown at elevated CO_2 levels versus ambient levels (Fonseca et al., 1997; Geiger et al., 1999; Larios et al., 2004). Furthermore, at elevated CO_2 levels, higher A (Robredo et al., 2007, 2010; Pérez-López et al., 2008, 2012b) may increase the proportion of total biomass allocated to underground tissues, especially to fine roots, which are the most important fraction for nutrient absorption and ultimately provide a higher N uptake (BassiriRad et al., 1996) even under salinity conditions. A higher value of A will increase the supplies of ATP and carbon skeletons, which in turn may also enhance the rate of GS activity (Geiger et al., 1999; Stitt and Krapp, 1999; Natali et al., 2009). Thus, regardless of salt stress, if N is not limiting, processes that promote N assimilation (N uptake and translocation, and NR and GS activities) may be increased, maintaining the N metabolism of plants grown in the presence of elevated CO_2 levels better than plants grown under ambient CO_2 conditions (Geiger et al., 1999; Stitt and Krapp, 1999; Natali et al., 2009; Robredo et al., 2011). Insight into the effects of salt and CO_2 on N partitioning and metabolism can be obtained using $\delta^{15}\text{N}$, which is sensitive towards environmental constraints and widely used to assess the effects of changing climate conditions on plant physiology (Peuke et al., 2006).

The effect of CO_2 or salinity on plants N metabolism has been studied separately for a large number of species but their interaction has barely been studied. In view of the fact that salinity decreases N metabolism and that elevated CO_2 decreases or enhances this metabolism, it seems logical to study what would happen if both conditions occurred together.

Barley is one of the most extensively cultivated crops worldwide, and its yield is promoted with an increase in CO_2 levels; however, despite its notable adaptation to water shortage and salt stress (Royo and Aragües, 1999; Sánchez-Díaz et al., 2002), salt stress reduces its productivity. Several authors have investigated the interaction between salinity and atmospheric CO_2 levels on A, water relations, oxidative stress, and redox status (Pérez-López et al., 2012a and literature therein). However, to our knowledge, no reports have evaluated the interactive effects of salt stress and CO_2 conditions on N acquisition, partitioning, reduction, and assimilation to provide an integrated picture of changes in these processes and their influence on relative growth rate (RGR; analysed from a nutrient perspective) and on the absolute growth of barley plants. This lack has prompted us to propose the following objectives: (1) to study the effects of salinity on N acquisition, reduction, and assimilation as well as the mechanisms by which elevated CO_2 levels modify these processes; (2) to analyse whether salt treatments and CO_2 conditions, singly or in combination, affect N content and $\Delta^{15}\text{N}$ in whole plant and in each of its organs; and (3) to evaluate the impact of salt-induced alterations in N metabolism on the growth of barley, whether elevated CO_2 levels alleviate this effect, and if so, by which mechanisms. To achieve these objectives, we determined the N uptake rate (NUR), N translocation rate (NTR), N content and $\Delta^{15}\text{N}$ in whole plant and in each of its organs, the NR and GS activities, and protein concentration. Photosynthetic N use efficiency (PNUE), whole-plant N use efficiency (NUE), RGR, and absolute growth were also measured in barley plants grown under non-salinized and salinized conditions at ambient ($350 \mu\text{mol mol}^{-1}$) or elevated ($700 \mu\text{mol mol}^{-1}$) CO_2 concentrations.

2. Materials and methods

Barley (*Hordeum vulgare* L. cv. Iranis) was grown in a Conviron E15 (Conviron, Manitoba, Canada) controlled environment growth chamber under ambient ($350 \mu\text{mol mol}^{-1}$) or elevated ($700 \mu\text{mol mol}^{-1}$) CO_2 levels from sowing throughout growth to the end of the experiment. Six seeds were sown in 2.5L pots containing a mixture of perlite/vermiculite (3:1, v/v) and maintained on a daily cycle of 14 h of light and 10 h of dark, with a relative day/night humidity of 70/80% and an average day/night temperature of 24/20°C. A combination of incandescent bulbs and warm-white fluorescent lamps (Sylvania F48T12SHO/VHO, Sylvania, Danvers, MA, USA) provided photosynthetically active radiation (PAR) of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$. Seedlings were watered every 2 days until the plants were 10 days old with Hoagland's solution (Arnon and Hoagland, 1940) containing 15 mM of N in the form of 6 mM KNO_3 , 4 mM $\text{Ca}(\text{NO}_3)_2$ and 1 mM $\text{NH}_4\text{H}_2\text{PO}_4$. The seedlings were then watered every 2 days with 250 ml 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})] for 14 days (Pérez-López et al., 2012b). At the end of the experimental period (28 days), the primary leaf was harvested and used for all measurements except for the determinations of the N concentration, the $\delta^{15}\text{N}$, the growth and the parameters derived from them. In these cases the whole plant was harvested and separated into leaves, stems, and roots.

2.1. Determination of N content, NUR, NTR, and $\delta^{15}\text{N}$

Plant N concentration (PNC) was determined from finely ground dry matter digested following the Kjeldahl method (AOAC, 1990). The dry matter came from a pooled sample from three independent experiments with three replications per treatment.

The NUR and NTR were calculated based on equations described by Franklin and Zwiazek (2004). NUR was described

Download English Version:

<https://daneshyari.com/en/article/4554586>

Download Persian Version:

<https://daneshyari.com/article/4554586>

[Daneshyari.com](https://daneshyari.com)