Journal of Plant Physiology 173 (2015) 120–129

Contents lists available at ScienceDirect

Journal of Plant Physiology

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

Physiology

High nitrate supply reduces growth in maize, from cell to whole plant

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ARTICLE INFO

Article history:
Received 2 April 2014
Received in revised form 7 June 2014
Accepted 29 June 2014
Available online 6 August 2014

Keywords:
1-Aminocyclopropane-1-carboxylic acid
Cytokinins
Nitrate
Ontogeny
Phytomer

ABSTRACT

Nitrogen (N) is an essential macronutrient that limits agricultural productivity, and both low and high N supply have been suggested to alter plant growth. The overall aim of this work is to study the impact of nitrate (NO_3^-) in maize yield and the possible causes that induce this alteration.

High NO_3^- doses did not increase the yield of maize grown neither in the field nor under controlled conditions. In fact, plants grown under controlled conditions for 45 days with NO_3^- concentrations over 5 mM showed a decrease in biomass production. This reduction was perceptible in shoots prior to roots, where phytomer expansion was reduced. Cell size and number were also reduced in the leaves of plants with high NO_3^-. This alteration was correlated with the increase of 1-aminocyclopropane-1-carboxylic acid in leaves, which was probably translocated from the roots in order to synthesize ethylene. Cytokinins (CKs) also showed a relevant role in this inhibitory effect, increasing in high NO_3^- plants with a reduction in root and shoot growth, inhibition of apical dominance and a strong decrease of leaf expansion, symptoms described previously as "CK syndrome". We propose that high NO_3^- inhibits maize growth by causing hormonal alterations that modify plant growth from cell to whole plant.

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Introduction

Nitrogen (N) is one of the most important nutrients for plants and affects their functions, from cell metabolism to growth (Marschner and Marschner, 2012; Scheible et al., 2004). Plant growth usually reacts in a positive way to the N application, showing increase in biomass production as N supply rises (Weligama et al., 2010). Plants with higher N availability have larger leaf area (Broadley et al., 2001; Vos et al., 2005), mainly due to higher leaf expansion rates (Lu et al., 2001).

Deficient N application has been widely studied and has been reported to reduce protein and chlorophyll content, and to alter N metabolism and photosynthesis (Lu et al., 2001; Zhao et al., 2005). Low N-supply also limits plant productivity as a consequence of a decrease in leaf area index (LAI), plant height and shoot weight (McCulough et al., 1994; Pandey et al., 2000). To avoid these consequences, large amounts of N fertilizer are applied to crops worldwide every year, especially in cereal production (Garnett et al., 2009). However, crops do not efficiently use the applied N-fertilizer and, as a consequence, the biomass production saturates after certain concentration (Berenguer et al., 2009), and an important amount of N is lost, contributing to environmental pollution (Gastal and Lemaire, 2002). Besides, high nitrate (NO_3^-) accumulation in plants has been related to some human diseases such as gastric cancer and blue baby syndrome (Knobeloch et al., 2000). Consequently, it is of great importance to improve the nitrogen use efficiency of plants. Thus, the identification of the most adequate N-fertilization rate for each crop and the limiting steps in the control of N uptake, assimilation and recycle during plant growth and development is essential (Jeuffroy et al., 2002; Lawlor, 2002), especially in crops of great interest such as maize (Hillier et al., 2005).

Nitrogen use efficiency (NUE) is the result of the interaction between two separate and independent traits: N uptake efficiency

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http://dx.doi.org/10.1016/j.jplph.2014.06.018
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and N utilization efficiency (Hirel et al., 2007; Wilkinson and Davies, 2010). For example, these traits have been described to change in wheat varieties (Wilkinson and Davies, 2010) which showed a decrease in the N uptake efficiency with the increment in the nitrogen supply, resulting in variations in the NUE. A reduction in NUE has also been observed in some C_4 species such as *Miscanthus* × *giganteus* (Danalatos et al., 2007). Furthermore, some studies have reported that excessive application of NO_3^- can reduce leaf area in *Nicotiana tabacum* (Stöhr, 1999), and whole plant growth in some other species such as *Brassica campestris* L., *Brassica chinensis* var. *Oleifera Makino et Nenotohas* and *Spinacia oleracia* L. (Chen et al., 2004). In addition, Arabidopsis roots exposed to NO_3^- supply over 10 mM, showed a significant decrease in the number of visible lateral roots (Zhang and Baldwin, 1997), this response being associated to the internal accumulation of NO_3^-. Regarding maize, some studies have also observed a negative effect of high doses in root growth (Guo et al., 2005; Tian et al., 2008), leaf expansion (Wilkinson et al., 2007) and whole plant development (Li et al., 1995). Even in field-like conditions, high N levels have been reported to reduce the production of maize (Pandey et al., 2000) and certain conifers such as *Cryptomeria japonica* and *Pinus densiflora* (Nakaji et al., 2001).

Maize is one of the most important crops and a C_4 plant that shows high NUE and fast growth rate. Due to NO_3^- supply being essential in its production, and the fact that the effect of its excessive application on the plant growth is controversial and not well understood, in this work we analyzed the effect of NO_3^- concentration in a range from suboptimal to overdose, both in the field and under controlled conditions. To this aim, the study of cell, leaf and plant growth could allow us to determine (i) the optimum nitrogen dose for maize grown in the field and under controlled conditions and (ii) the incidence of the N dose in the ontogeny and kinetic of the phytomer expansion and its effect on plant growth. Besides, because the N assimilation and plant development are regulated by phytohormones, that coordinate N demand and acquisition (Kiba et al., 2011), the simultaneous analysis of physiological and morphological traits together with hormone changes would give us (iii) additional information about their roles in plant development under different NO_3^- supply.

Materials and methods

Field experiment

Commercial seeds of maize (*Zea mays* L. cv. Franki and cv. Crazy) (Caussade, France) were sown on May 23rd 2007 in the town of Gauna, province of Alava, Spain. Background fertilization was 0:14:14 (N:P:K). Soil N content was 0.17%. After sowing, a top dressing was supplied consisting on four different N fertilization doses (0, 100, 200 and 400 kg ha^{-1}). The application of nitrogen doses up to 200 kg ha^{-1} is a common practice in field experiments involving maize plants (Ma and Dwyer, 1998; Ramos et al., 2009). However, depending on the area and irrigation system, maize N uptake can be over 250–300 kg ha^{-1} (Berenguer et al., 2009). Moreover, in certain regions of Spain, such as the Ebro Valley, N fertilization in maize cropping can be as high as 300–350 kg ha^{-1} (Sisquella et al., 2004). In order to provide the entire amount of N that plants could potentially uptake, and also to adjust to the local cropping management, N treatment of 400 kg ha^{-1} was also included. After 145 days (October 15th), harvest was performed to determine biomass production. Nitrogen use efficiency (NUE) was calculated for the 100, 200, and 400 kg ha^{-1} N doses following the definition for the "partial factor productivity of applied nutrient" provided by Snyder and Bruulsema (2007):

$$\text{NUE} = \text{kg biomass produced} \times \text{kg total N applied}^{-1} \quad (1)$$

Growth chamber experiment

Franki variety was selected for the growth chamber experiment. Maize seeds were germinated in moistened paper, kept at room temperature in the dark. When maize radicles reached 2 cm long, seedlings were transplanted to 9 L pots (25 cm ⌀), filled with perlite–vermiculite (1/1, v/v). Plants were grown under a 14 h photoperiod at 25/20 °C temperature and 70/80% relative humidity (day/night). The light intensity at the canopy was 500 μmol m^{-2} s^{-1} photons as described by Garnett et al. (2013).

Starting five days after germination, plants were irrigated three times per week with 500 mL of solution based on Hoagland sol. 1 (13 mM NO_3^-) at pH = 5.7 (Cerny et al., 2013). In order to cope with a wide range of NO_3^- supply different concentrations based on Hoagland solution were applied (2.5, 5, 10, 15 and 30 mM nitrate). 2.5 mM of NO_3^- was chosen as the minimal dose, which allowed proper plant development without suffering the symptoms associated to severe N deprivation. Accordingly, 2.5 and 3 mM are considered medium (McCulough et al., 1994) or base level (Schmelz et al., 2003). The 30 mM treatment was included to study the effect of an extreme, but still plausible, NO_3^- concentration. In fact, in certain crop-growing areas the NO_3^- present in the soil can reach 20 mM concentration (Andrews, 1986). Moreover, concentrations around 30 mM of N or higher have been used in plant culture, either as control (Ciompi et al., 1996) or as high N concentration (Marín et al., 2011).

The 15 mM solution contained 1.181 g L^{-1} $Ca(NO_3)_2$, 0.506 g L^{-1} KNO_3, 0.115 g L^{-1} $NH_4H_2PO_4$, 0.493 g L^{-1} $MgSO_4$, 2.83 mg L^{-1} H_3BO_3, 1.81 mg L^{-1} $MnCl_2$, 0.22 mg L^{-1} $ZnSO_4$, 0.08 mg L^{-1} $CuSO_4$, 0.11 mg L^{-1} Na_2MoO_4 and 10.06 mg L^{-1} Fe chelate (Exclusivas Sarabia, S.A., Alpicat, Spain). The solution containing 30 mM of NO_3^- was prepared increasing the amount of KNO_3 applied. In the watering solutions below 15 mM of NO_3^-, KNO_3 and $Ca(NO_3)_2$ were replaced by $CaCl_2$, $CaSO_4$ and K_2SO_4, according to Reed and Hageman (1980) and Stöhr (1999).

A minimum of five plants per treatment was used and the study was repeated six times.

Sampling and parameter determination

Plant fresh material was harvested at 15, 22, 30, 37 and 45 days after germination. Phytomer was used as the structural unit for studying the plant development and consisted of the leaf blade, its sheath and its internode (Fig. 2B) (Birch et al., 2007; Fournier and Andrieu, 2000). Fully expanded phytomers were numbered from eldest to youngest. Length and width of the leaf-blade in each phytomer and its collar height (Fig. 2B) were measured. Leaf-blade area and total leaf area were measured using a Li-3100 Area Meter (Li-Cor Inc., Lincoln, NE, USA). Plants of each treatment were divided into leaf, stem and root fraction, and dried for 48 h at 80 °C to determine dry weight (DW, g). Leaf mass fraction (LMF, g g^{-1} plant) and stem mass fraction (SMF, g g^{-1} plant), and shoot to root ratio (g g^{-1}) were also calculated from its DW. Leaf area rate (LAR, m^2 kg^{-1} plant) and specific leaf area (SLA, m^2 kg^{-1}) were determined using the following equations (Hunt, 2003):

$$\text{LAR} = \frac{\text{total leaf area}}{\text{total plant DW}} \quad (2)$$

$$\text{SLA} = \frac{\text{total leaf area}}{\text{total leaf DW}} \quad (3)$$

The relative expansion rate (RER) of each phytomer was calculated as follows:

$$\text{RER} = \frac{\text{Ln length } t_n - \text{Ln length } t_{n-1}}{t_n - t_{n-1}} \quad (4)$$

where t_n is the n time.

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