



Nitrate supply induces changes in polyamine content and ethylene production in wheat plants grown with ammonium

Maria Garnica^a, Fabrice Houdusse^a, Jean Claude Yvin^c,
Jose M. Garcia-Mina^{a,b,*}

^aCIPAV-Timac Agro Int Roullier Group, Poligono Arazuri-Orcoyen, C/C No. 32, 31160 Orcoyen (Navarra), Spain

^bDepartment of Chemistry and Soil Chemistry, Faculty of Sciences, University of Navarra, P.O. Box 273, 31080 Pamplona (Navarra), Spain

^cR&D Timac Agro Int., S Malo, France

Received 19 April 2008; received in revised form 12 June 2008; accepted 13 June 2008

KEYWORDS

Nitrate;
Ammonium;
Polyamines;
Ethylene;
Wheat

Summary

In order to explore the mechanisms of nitrate's beneficial effect on ammonium-grown plants, we investigated the effects of nitrate on free and conjugated polyamine plant content and ethylene biosynthesis in wheat (*Triticum aestivum* L.) plants grown with ammonium nutrition. Two different doses of nitrate (100 μ M and 5 mM) were supplied to ammonium-fed plants, in order to determine whether the effects of nitrate require significant doses (nutritional character), or can be promoted by very low doses (pseudo-hormonal character).

Our results showed that nitrate's effects on putrescine, spermidine and spermine contents of ammonium-grown plants tended to follow the pattern associated with strict nitrate nutrition. Both low (100 μ M) and high (5 mM) nitrate doses caused a rapid and significant increase in free spermidine content in roots and shoots, which was well correlated with reduced root ethylene production. In shoots, this increase in free spermidine was correlated with changes in the conjugation pattern, while in roots these changes appear to be due to alternative mechanisms. On the other hand, no clear relationship between the supply of a lower dose of nitrate (100 μ M) and a reduction of free putrescine content was observed. With higher doses of nitrate (5 mM) we observed a reduction of free putrescine content that was well correlated with increases in its conjugated forms. In conclusion, nitrate's effects on putrescine,

Abbreviations: N, nitrogen; NH_4^+ , ammonium; NO_3^- , nitrate; DW, dry weight; NA, nitrate-ammonium; PA, polyamine; PAs, polyamines; Put, putrescine; Spd, spermidine; Spm, spermine; PCA, perchloric acid; SAM, S-adenosylmethionine; SAMDC, SAM decarboxylase.

*Corresponding author at: CIPAV-Timac Agro Int Roullier Group, Poligono Arazuri-Orcoyen, C/C No. 32, 31160 Orcoyen (Navarra), Spain.

E-mail address: jgmina@timacagro.es (J.M. Garcia-Mina).

spermidine and spermine contents of ammonium-fed plants tended to follow the pattern associated with strict nitrate nutrition, corroborating its beneficial effect.
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Introduction

Nitrogen (N) is required in large quantities by plants and is one of the major factors limiting plant growth. It is taken up by the roots principally in the forms of nitrate (NO_3^-) and ammonium (NH_4^+), the most abundant N forms present in soil (Marschner, 1995). NH_4^+ derived from soil solution, as well as NH_4^+ derived from NO_3^- reduction, deamination of nitrogenous compounds and other internal processes are rapidly assimilated by the glutamine synthetase–glutamate synthase pathway. Taking into account both uptake and assimilation costs, NH_4^+ should be preferred to NO_3^- as a N source. However, NH_4^+ nutrition usually has deleterious effects on plant growth and can result in toxicity symptoms in many plants (Britto and Kronzucker, 2002).

A number of studies have shown that the negative effects associated with NH_4^+ nutrition in certain plant species are corrected by the presence of NO_3^- in the nutrient solution (Britto and Kronzucker, 2002; Cruz et al., 2003). Some authors have reported that this effect was also observed when very low concentrations of NO_3^- were present in the nutrient solution (Rahayu et al., 2005). Some have suggested that NO_3^- may function as a signal compound triggering plant growth responses (Zhang et al., 1999; Forde and Clarkson, 1999; Stitt, 1999; Wang et al., 2000). Several studies have shown that a long- and short-term NO_3^- supply to NH_4^+ -fed plants stimulates leaf growth via interaction with root-derived cytokinins acting as long distance signals (Rahayu et al., 2005). However, nature of the biochemical and physiological events responsible for these beneficial effects of NO_3^- on NH_4^+ nutrition remains unknown. Some studies suggest that these effects might be related to changes in the physiological pH (Babourina et al., 2007), the maintenance of appropriate carboxylate levels in plants (Feng et al., 1998), or to specific changes in the levels of certain plant hormones, such as polyamines (PAs), as well as in proline content (Houdusse et al., 2005).

With respect to polyamine (PA) metabolism, Houdusse et al. (2005) reported that free putrescine (Put) content in leaves was well correlated with the intensity of the negative effects of NH_4^+ on the development of wheat and pepper plants. Other studies have also indicated that a way to reduce free NH_4^+ levels in plant tissues could be its

conversion in free Put (Triantaphylides et al., 1993). A number of studies have shown that free Put accumulation can cause negative effects on plant development, including potassium leakage, protein loss, depolarization of membranes, and tissue necrosis (Tiburcio et al., 1990).

Houdusse et al. (2005) also observed that plants receiving mixed N nutrition containing NO_3^- and NH_4^+ exhibited clear decreases in the free Put content when compared with those fed with strict NH_4^+ nutrition, in both roots and leaves of wheat and pepper plants. This result was also related with reduced values of the Put/(spermine (Spm)+spermidine (Spd)) ratio (Houdusse et al., 2005). Other studies have reported that reduction in the Put/(Spm+Spd) ratio could be a protective factor under stress conditions (Bouchereau et al., 1999; Capell et al., 2004). The beneficial action of NO_3^- in correcting the negative effects of NH_4^+ nutrition on plant growth would involve the reduction of free Put accumulation in plant tissues and, as a consequence, an increase in Spd and Spm content in both roots and shoots.

Apart from biosynthesis, PA levels may be modulated by conjugation either with small molecules like hydroxycinnamic acids (soluble conjugated PAs (perchloric acid (PCA)-soluble bound)) or with high-molecular-mass substances such as hemicelluloses, lignin, and proteins (insoluble conjugated PAs (PCA-insoluble bound)). It has been documented that these conjugated forms of PAs appear to be involved in the regulation of various physiological and biochemical processes in plants (Mauricio et al., 1999; Piqueras et al., 2002). In recent studies, conjugated forms of PAs have been considered as possible members of the plant defense system against stress (Martin-Tanguy, 2001). They may participate in the scavenging of oxygen radicals and in H_2O_2 generation in cells during PA oxidation (Shevyakova et al., 2006). In addition, they may act as transport forms or as storage forms of PAs from which free bases, which are known to be the active forms, may be released, thus regulating the free PA-titer (Martin-Tanguy, 1997, 2001). Finally, it has also been reported that conjugated forms of PAs can interact with cell wall components under stress conditions, stabilizing plasma membranes (Bagni and Pistocchi, 1991). However, many functions of conjugated forms of PAs are still unclear.

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