



Can NO Signaling and Its Metabolism Be Used to Improve Nutrient Use Efficiency? Toward a Research Agenda

Agustina Buet^{1,2}, Melisa Luquet³, Guillermo E. Santa-María⁴ and Andrea Galatro^{3*}

¹ Centro de Investigaciones en Toxicología Ambiental y Agrobiotecnología del Comahue (CITAAC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Universidad Nacional del Comahue, subsele Instituto de Biotecnología Agropecuaria del Comahue (IBAC), Cinco Saltos, Argentina, ² Facultad de Ciencias Agrarias y Forestales (FCAYF), Universidad Nacional de La Plata (UNLP), La Plata, Argentina, ³ Instituto de Fisiología Vegetal (INFIVE), Universidad Nacional de La Plata (UNLP)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), La Plata, Argentina, ⁴ Instituto Tecnológico Chascomús (INTECH), Universidad Nacional de San Martín (UNSAM)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Chascomús, Argentina

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Christian Lindermayr,
Helmholtz Association of German
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Francisco J. Corpas,
Department of Biochemistry, Cell and
Molecular Biology of Plants,
Experimental Station of Zaidín,
Spanish National Research Council
(CSIC), Spain
Halley Oliveira,
State University of Londrina, Brazil

*Correspondence:

Andrea Galatro
avgalatro@gmail.com;
andrea.galatro@agro.unlp.edu.ar

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INTRODUCTION

One important issue to be faced by modern agriculture is ensuring an efficient use of the essential nutrients taken up from the soil by crops, thus helping to reduce the economic costs and by-side environmental effects derived from addition of fertilizers, which -frequently- involve the use of non-renewable resources. Improving use efficiency of the major nutrients contained in these fertilizers, nitrogen (N), phosphorus (P) and potassium (K), can be afforded through multiple strategies and must be thought in concert with the prevalence of a panoply of biotic and abiotic stresses. Therefore, simultaneous attention must be paid to the signaling network involved in setting Nutrient Use Efficiency (NUE) and to the acclimation of plants to a wide range of environments.

Nitric Oxide (NO) has been shown to influence some aspects of N, P and K nutrition as well as the response of plants to several stress conditions (Buet et al., 2019; Kolbert et al., 2019). The possibility to use NO metabolism/signaling to improve NUE has been recently contemplated (Del Castello et al., 2020). However, there is considerable uncertainty regarding how NO manipulation can be readily used to improve NUE. In this opinion article, we highlight the unknowns that must be known in order to make that use feasible while proposing some priorities for a research agenda. Given the various roles covered by NO in plants, special attention should be paid to the occurrence of unwanted collateral effects derived from NO manipulation. We emphasize that the use of NO to improve NUE will require deep knowledge on the signaling network involved, as well as a suitable quantitative assessment of NUE and its components.

NUE: COMPONENTS AND MECHANISMS

NUE is an increasingly used concept that refers to the yield, or dry matter accumulation, relative to the availability of a given nutrient in the soil solution. It can be decomposed into Nutrient Acquisition Efficiency (NAE) and Nutrient Utilization Efficiency (NUE). NAE informs on the amount of nutrient captured by plants relative to nutrient availability in the soil, while NUE informs on the yield (or dry matter accumulated) per unit of nutrient incorporated (Rose and Wissuwa, 2012; Santa-María et al., 2015).

Several plant traits contribute to determining NAE; including the root growth pattern, the symbiotic and non-symbiotic relationships with soil microorganisms, the release of compounds that modify nutrient availability, and the activity of the transporters in the root absorbing zone. Current knowledge indicates that NUtE involves traits related to the distribution of nutrients and dry matter among different organs, the capacity to modify the metabolism, and the partial substitution of an element by a related one. These traits could involve several mechanisms, extensively revised for N, P and K (Veneklaas et al., 2012; Cormier et al., 2016; White et al., 2021).

NUE: THE NEED TO QUANTIFY THE IMPACT OF NO

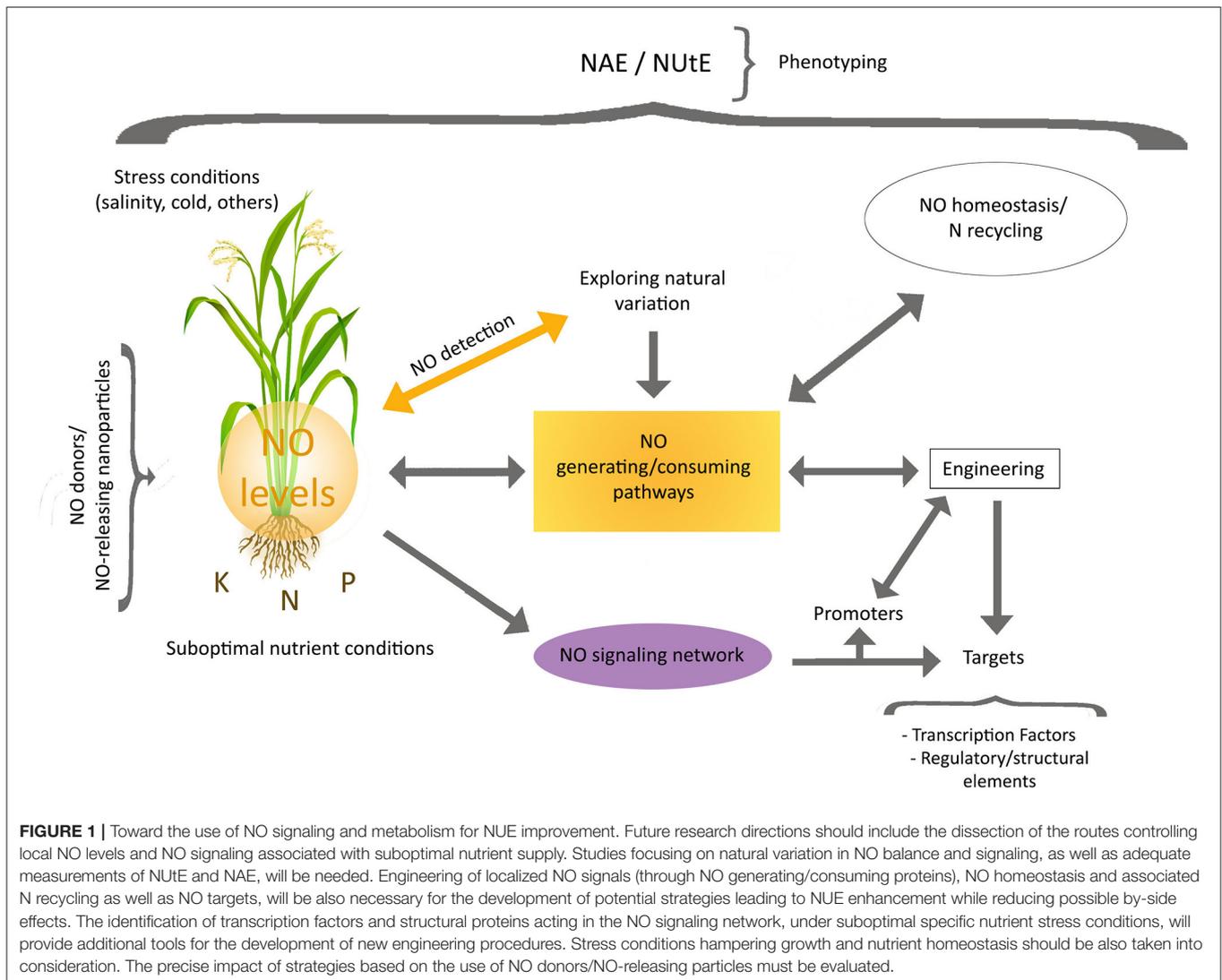
Available information indicates that NO influences many processes underlying traits related to NUE. As an example, it has been shown that, under conditions of variable N supply, root growth, N uptake and assimilation are influenced by NO (Frunghillo et al., 2014; Sun et al., 2015; Balotf et al., 2018). Reciprocally, NO is coupled with N metabolism, as NO can be generated from nitrite, arising from N assimilation, and from arginine arising from N metabolism. Moreover, NO generation may be affected by the forms (NO_3^- or NH_4^+) and the levels of N supply (Buet et al., 2019), potentially influencing NUE. Evidence also supports a role of NO on key responses to low P supply (Wang et al., 2010; Zhu et al., 2017; Ramos-Artuso et al., 2018), and in K nutrition (Chen et al., 2016). In addition, proteins likely involved in setting NUE are subjected to NO post-translational modifications such as occur with the P-transporter PHT3;1 (Fares et al., 2011), and -knowing the cysteine residues involved- glutamine synthetase (Silva et al., 2019) and S-nitrosoglutathione Reductase 1, GSNOR1 (Frunghillo et al., 2014; Guerra et al., 2016). NO can also affect the expression of NUE-likely-related transcripts, such as those coding for nitrate reductase, other enzymes of the N assimilation pathway (Balotf et al., 2018), and the P-transporter *OsPT2* (Zhu et al., 2017).

Despite the evidence indicating that NO influences mechanisms underlying nutrient acquisition and utilization, there are scarce measurements of NAE and NUtE in the framework of NO research (e.g., Del Castello et al., 2021; Gautam et al., 2021). Thus, the precise quantitative influence of NO on them remains mostly unknown. This should prompt to perform measurements of these efficiencies, an aspect that needs the use of adequate phenotyping protocols. In this regard, NAE must be preferentially evaluated with plants grown in soil, as interactions with soil matrix and microorganisms could be relevant. Measurements of NUtE must be preferentially performed with growth systems that help to avoid large disparities in nutrient accumulation (Rose and Wissuwa, 2012), accompanied by the use of appropriate estimators (Santa-María et al., 2015). Performing measurements of NAE and NUtE with validated phenotyping protocols in the context of NO research constitutes the first item of our research agenda.

NUE IMPROVEMENT: THE NEED TO KNOW THE BALANCE OF ENDOGENOUS NO LEVELS AND NO SIGNALING NETWORKS

The impact of NO signaling and metabolism to improve NUE will depend on the way by which endogenous NO levels and their subsequent actions are set in a particular environment. This is a complex and essentially unknown issue for most nutritional conditions and, as described for several processes, likely involves interactions with other signals such as reactive oxygen species and hormones (Kolbert et al., 2019). It should be noticed that NO may exert its actions in a compartmentalized way, involving a delicate equilibrium between NO generation and consumption, which could be critical to set a given biological outcome (Hancock, 2019). The precise contribution of NO generation and consumption pathways to determine NO levels under growth conditions compatible with adequate measurements of NAE and NUtE remains essentially unknown and constitutes a second component of the research agenda. The relevance of those pathways in setting NUE should not be underestimated as exemplified by the effect of variable nitrate supply on maize root growth, where NO production and scavenging, associated with a coordinated spatiotemporal expression of nitrate reductase and non-symbiotic hemoglobins (involved in NO generation and consumption, respectively), finally contribute to defining primary root growth (Trevisan et al., 2011; Manoli et al., 2014). Noticeably, the effects displayed by NO have been shown to depend not only on the levels of nutrient supply, but also on the interaction with other environmental conditions (Du et al., 2016).

NUE relates the economy of mineral elements and carbon. Maintenance of NO generation within a narrow range is necessary to optimize growth (Sánchez-Vicente et al., 2019) while less is known about the effect of NO balance on the control of the elemental composition (Babasheikhali et al., 2020; Sohag et al., 2020). The addition of NO donors, as well as the use of mutants or transgenic plants displaying enhanced NO production in several tissues, would lead to NO imbalances, followed by a cascade of NO actions that finally are integrated into a whole plant outcome. The occurrence of multiple NO induced events is indicated by transcriptome studies unveiling that exogenous NO affects the expression of many transcription factors (Hussain et al., 2016; Imran et al., 2018), and can also influence the activity of some of them as shown by *in vitro* studies (Serpa et al., 2007; Tavares et al., 2014). Besides, work with the *nox1* mutant -displaying enhanced NO production-disclosed relevant modifications in the proteome (Hu et al., 2014). In this context, it should be considered that low levels of different nutrients—or other stress conditions—could coexist, involving an interplay among signaling cascades. Therefore, particularly following exogenous NO treatments, the possibility of affecting more than a single signaling cascade exerting non-predictable impacts on traits contributing to different stress conditions should be contemplated. This can be partially illustrated, considering that the addition of certain NO donors could lead—in some plants, under particular growth conditions—to enhanced N, P and/or K uptake (Sun et al., 2015; Ramos-Artuso et al., 2018; Alnusairi et al., 2021). However, in



some environments these NO donors may negatively impact on the main systems determining K influx (Xia et al., 2014; Oliferuk et al., 2020). On the other hand, abiotic stresses like salinity and cold, hamper the nutrition of some elements, and addition of NO could help plants to reduce detrimental effects exerted on growth and the accumulation of certain nutrients (Sohag et al., 2020; Alnusairi et al., 2021). Therefore, in deep studies on NO signaling cascades (and specially their connections) for interacting levels of nutrient supply and stress conditions should be reinforced in the research agenda.

Having in mind all the issues just discussed, it seems unlikely that NO donors can mirror the specific acclimation roles of endogenous NO during nutrient deficiencies, and interactive no obvious effects on NUE for different elements may be expected. Nevertheless, the possibility to use NO-releasing nanoparticles should be not excluded as they may deliver NO in a more controlled way (as compared to free forms), promoting growth under particular stress conditions

(Silveira et al., 2021). Similar considerations may apply for specific transgenic plants. Considering the issues here mentioned, another aspect to be incorporated into the research agenda is the need to provide an integral evaluation of the plant performance, especially its stability across environments, for any NO manipulation approach.

FUTURE DIRECTIONS

In the context of NUE improvement, studies on the endogenous NO signaling pathways operating under conditions of suboptimal nutrient supply will be relevant, as they may disclose the targets of NO action, which should be complemented by the identification of the routes leading to set local NO levels (Figure 1). The subsequent engineering of localized NO signals, as well as of the NO homeostasis and associated N recycling (Del Castillo et al., 2020), along with that of NO targets, could be

the base of future strategies for NUE enhancement. A strategy based on alteration of localized NO levels will need innovative technical procedures to estimate them, including the use of genetically encoded sensors (Safavi-Rizi, 2021). The alteration of NO levels could be achieved by the introgression of NO generating/consuming proteins under the control of well-suited promoters, acting under specific nutritional conditions, thus reducing the by-side effects emerging from uncontrolled NO use. Introgression of proteins affecting NO balance, may also result in N metabolism modifications, as shown in *Arabidopsis* plants expressing *SyNOS*, from *Sinechococcus*, which besides to generate NO from arginine, mediates its conversion to nitrate leading to an enhancement of NUE under low N supply (Del Castello et al., 2021). In addition, identification of transcription factors and structural proteins acting downstream in the NO signaling network, elicited by specific nutrient stress conditions, may be used for a wide range of approaches to express or edit proteins contributing to traits for enhanced NAE and/or NUtE. All these items must be also included in the research agenda here outlined.

Furthermore, screening of large collections, under variable nutrient supply conditions, using either mutagenized plants or high-diversity panels, may help to identify key elements involved in NO generation and signaling yet unknown. The use of the first procedure led to uncover the role of pyridoxal in the control of K transport (Xia et al., 2014). Regarding the second one, a recent genome-wide association study using a panel of genotyped barley accessions uncovered several marker-associations with NO release (Nagel et al., 2019). To our knowledge no studies have been conducted to disclose the existence of natural variation in NO release for crop plants deprived of major nutrients and to examine its potential association with NUE variation

among genotypes. This is an additional issue to be afforded by future research.

In conclusion, the extent to what and how NO signaling/metabolism can be manipulated to impact on NUE improvement will greatly depend on the accomplishment of a detailed research agenda just outlined here (Figure 1). This will require careful experimental designs and the use of suitable protocols of phenotyping across multiple environments.

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