Plant Signaling & Behavior 9, e28290; March; © 2014 Landes Bioscience

NO signaling is a key component of the root growth response to nitrate in *Zea mays* L.

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Keywords: *Zea mays* L., nitrate, root, transition zone, nitric oxide

Abbreviations: cPTIO, 2-(4-Carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide; IAA, indole-3-acetic acid; SNP, sodium nitroprusside

Roots are considered to be a vital organ system of plants due to their involvement in water and nutrient uptake, anchorage, propagation, storage functions, secondary metabolite (including hormones) biosynthesis, and accumulation. Crops are strongly dependent on the availability of nitrogen in soil and on the efficiency of nitrogen utilization for biomass production and yield. However, knowledge about molecular responses to nitrogen fluctuations mainly derives from the study of model species. Nitric oxide (NO) has been proposed to be implicated in plant adaptation to environment, but its exact role in the response of plants to nutritional stress is still under evaluation. Recently a novel role for NO production and scavenging, thanks to the coordinate spatio-temporal expression of nitrate reductase and non-symbiotic hemoglobins, in the maize root response to nitrate, has been postulated. This control of NO homeostasis is preferentially accomplished by the cells of the root transition zone (TZ) which seems to represent the most nitrate responsive portion of maize root. The TZ is already known to function as a sensory center able to gather information from the external environment and to re-elaborate them in an adequate response. These results indicate that it could play a central role also for nitrate sensing by roots. A lot of work is still needed to identify and characterize other upstream and downstream signals involved in the "nitrate-NO" pathway, leading to root architecture adjustments and finally to stress adaptation.

To search for nutrients and water, roots need to efficiently explore large soil volumes. To this aim they generate complex root systems, allowing them to maximize their resource allocation efficiency.[1]

Despite the vital importance of roots, the difficulty in accessing intact root systems for analysis, particularly under field conditions, have slowed down the breeding programs for plant's adaptation to environmental restrictions.[2,3] The capacity of plants to take up nutrients and water is mainly determined by changes in the architecture of the root system.[1]

Three major processes affect the overall architecture of the root system: the rate of cell division, the rate of cell differentiation, and the extent of expansion and elongation of cells.[4-6] Disturbs in any of these 3 processes can affect the whole root-system architecture and the capacity of plants to survive and develop in adverse environments (Giehl et al.[7] and references therein).

The root system results from the coordinated control of both genetic endogenous programs (regulating growth and organogenesis) and the action of abiotic and biotic environmental stimuli.[8,9] The dynamic control of the overall root system architecture (RSA) throughout time finally determines root plasticity and allows plants to efficiently adapt to environmental constraints.[10]

The soil-environment from which plants extract nutrients and water is extremely heterogeneous, both spatially and temporally.[11] Among the nutrients present in soil, nitrate (NO_3^-) may vary by an order of magnitude within centimeters or over the course of a day.[12] The effects of NO_3^- on the root system are complex and depend on several factors, such as the concentration available to the plant, the endogenous nitrogen status and the sensitivity of the species.[10,13,14]

A considerable part of the studies aimed to unravel the mechanisms controlling RSA growth and development in response to nitrate have been focused on lateral roots (LR),[8,13,15-20] while the nitrate-regulation of the primary root growth is still unclear. Beside NO_3^-, auxin has been demonstrated to strongly affect and control the LR development,[21-24] and an increasing number of studies suggests an overlap between auxin and NO_3^- signaling pathways in controlling LR development.[25-33]

NO_3^- has a Doubtful Role in Regulating the Growth of Primary Roots

Despite the high amount of reports published on nitrate effects on root elongation, the lack of univocal results makes it difficult to clearly decipher this response (**Table 1**). In *Arabidopsis thaliana*, inhibition of primary root growth has been observed when nitrate is applied homogeneously at high concentrations (50 mM) for 7 d, but not in a range between 0.1 and 10 mM.[35] On the contrary, in this same species Linkohr et al.[36] showed an inhibition of primary root elongation with the increase of nitrate concentration already beyond 0.01 mM, but in this case seedlings were

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Submitted: 02/19/2014; Accepted: 02/19/2014; Published Online: 03/10/2014
Citation: Trevisan S, Manoli A, Quaggiotti S. NO signaling is a key component of the root growth response to nitrate in Zea mays L. Plant Signaling & Behavior 2014; 9:e28290; PMID: 24613869; http://dx.doi.org/10.4161/psb.28290

Table 1. Overview of the papers reporting results on primary root (PR) response to nitrate treatments

Authors	Species	Treatments	Effect on PR length
Zhang and Forde[34]	*Arabidopsis thaliana*	Seedlings were grown on agar plates containing a range of NO_3^- concentration (0.01–100mM) and the lengths of the primary roots were measured after 14d.	No effects
Signora et al.[35]	*Arabidopsis thaliana*	Seedlings were grown on agar plates containing a range of NO_3^- concentrations (0.1–50mM). The lengths of the primary roots were recorded after 7d.	No effects (0.1–10mM) Inhibition (> 50mM)
Linkohr et al.[36]	*Arabidopsis thaliana*	Seedlings were grown either for 17 or 18d on agar plates containing a range of NO_3^- concentrations (0.01–1.0mM). The lengths of the primary roots were collected after the treatments.	Inhibition
Walch-Liu and Forde[13]	*Arabidopsis thaliana*	Primary root growth was measured 9d after transfer of 5-d-old seedlings to segmented plates where NO_3^- (0.05–5mM) was present only in the bottom segment (localized treatments).	Stimulation
Gifford et al.[37]	*Arabidopsis thaliana*	Seedlings were grown on agar plates containing a range of NO_3^- concentration (0–20mM). The primary root lengths were measured after 12d.	Stimulation
Celis-Arámburo et al.[14]	*Capsicum chinense* Jacq.	Seedlings were grown on agar plates with 0.01mM NO_3^- and transferred to segmented. NO_3^- concentrations in the middle segment were adjusted to 0.01–10mM (localized treatments). For the homogeneous treatment the concentration was 1mM NO_3^-. The primary root lengths were recorded after 10d.	Inhibition
Yendrek et al.[38]	*Medicago truncatula*	Plants were grown on a N-free medium for 1 wk, transferred to plates with increasing concentrations of NO_3^- (1–20–50mM) and grown for 3 wk. The lengths of the primary roots were recorded after the treatments.	Inhibition
Tian et al.[39]	*Zea mays* L.	Plants were grown in nutrient solution containing several NO_3^- concentration (0.05–20mM). The lengths of the primary roots were recorded after 12d.	Inhibition (> 5mM)
Tian et al.[40]	*Zea mays* L.	Seedlings were incubated in the solutions containing different concentrations of NO_3^- (0.05–20mM) and the root length was measured after 12d of incubation.	No effects (0- 0.5mM) Inhibition (> 5mM)
Zhao et al.[41]	*Zea mays* L.	Seedlings were grown in varying concentrations of NO_3^- (0.1–10mM) for 7d and then exposed to 0.1 and 1mM NO_3^- for 48h. The root length was measured after the incubation.	Inhibition
Manoli et al.[68]	*Zea mays* L.	Primary root growth of 8-d-old seedlings grown in 6 different solutions (1mM NO_3^-, - NO_3^- and NO-donors/scavengers) were monitored for 24–48h.	Stimulation

grown in the nutrient medium either for 17 or 18 d. This is in contrast with results previously obtained by Zhang and Forde,[34] which did not observe changes in primary root length in a range of nitrate concentrations from 0.01 mM to 100 mM.

However, if nitrate supply was localized only to the apex, primary root growth of a number of *Arabidopsis* accessions was significantly stimulated, even if to a different extent according to the line responsiveness.[13] More recently Gifford et al.[37] demonstrated a stimulatory effect on primary root elongation in *Arabidopsis* seedlings grown for 12 d on a nitrate concentration ranging from 0 to 20 mM. Conversely, a reduction of primary root growth has been observed in both *Capsicum chinense* Jacq.,[14] and *Medicago truncatula*[38] in response to a prolonged exposure to nitrate.

In maize (*Zea mays* L.) a consistent inhibitory effect on primary root length was observed by Tian and co-authors after 12 d of growth at a nitrate concentration of 20 mM.[39] A few years later a more detailed study was published by the same authors who demonstrated that nitrate concentrations lower than 0.5 mM had no effect on elongation of primary, seminal, and crown roots, while concentrations above 5 mM affected more significantly the root elongation after 12 d of treatment.[40] Moreover, by investigating the effect of different nitrate concentrations on root cell sizes, they found that high concentrations of nitrate had no effect on the length of the meristem, but did result in reduced cell elongation in the root elongation zone. Interestingly, the different types of roots considered in this study displayed different sensitivities to high nitrate, suggesting a specific regulation for each of them.[40]

Unlike what is known on the nitrate regulation of lateral root development, the mechanisms underlying the nitrate effects on primary root elongation are still controversial and poorly known. Future studies are thus needed to try to shed light on this aspect that could highly affects plant adaptation to an external environment characterized by a spatio-temporal non constant nutrient accessibility.

The Root Transition Zone

The root apex represents the first part of the plant getting in touch with unknown regions of the soil, and it functions as a dynamic sensory organ, able to both perceive the external environment and to adequately reorganize the root growth in response to the stimuli received.[42]

In 1990 Baluška et al.[43] invented the term transition zone to describe a unique part of the maize root apex, in which cells after leaving the meristem and before entering the elongation zone undergo slow isotropic-like growth, but do not still elongate, in fact resembling meristematic cells in many aspects. In particular, the apical part (distal) of this region seems to be characterized mainly by cells that optionally can reenter the cell cycle, whereas cells of the basal (proximal) part of this zone are able to readily enter into the fast cell elongation region.[42,44,45] This developmental feature could be differentially regulated at the opposite root flanks, providing the root apices with an effective mechanism to re-orientate growth in response to environmental stimuli.[44]

The transition zone is a unique zone being competent for integration of diverse endogenous and exogenous signals, and translating them into adaptive differential growth responses. It plays crucial functions for the perception and response to a range of external factors, as for example mechanical stimuli[42] and aluminum toxicity.[46-49]

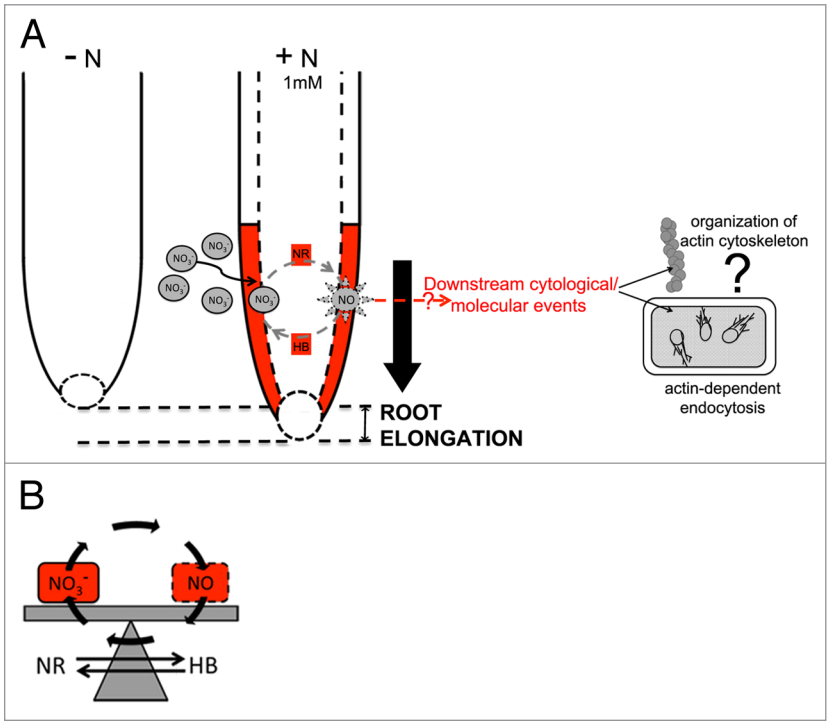

Figure 1. Model of the NO-mediated nitrate regulation of primary root elongation. (**A**) The transfer of seedlings from a NO_3^--deprived media to a NO_3^--supplied solution results in a elongation of the primary root. The stimulatory effect of NO_3^- (1mM) was demonstrated to be dependent on the control of nitric oxide (NO) homeostasis thank to the coordinate regulation of cytosolic nitrate reductase (NR) and non-symbiotic hemoglobins (nsHbs) (**B**).[67,68] The preferential localization and the strong transcriptional responsiveness of both NR and nsHbs in the transition zone of the apex straightened the hypothesis of a role of this root portion in translating the environmental stimuli in developmental response.[67,68] Because of the role of NO in several cytoskeleton-mediated processes in plants,[76-83] the actin-dependent endocytosis and the organization of the actin cytoskeleton are proposed as candidates in transducing the NO-dependent nitrate regulation of root elongation.

This capability seems to be, at least in part, linked to the complex system of a polar auxin transport circuit.[42] Actually, since 1993 it has been evidenced that cells belonging to this zone are strongly auxin-responsive and accomplish dramatic rearrangements of the cytoskeleton, being subjected to a series of fundamental changes in their cytoarchitecture.[50]

A recent study conducted on maize demonstrated that the transition zone plays central roles in both sensing and adapting to root hypoxia.[51] The authors also observed that the oxygen deprivation of roots induces local NO emission in the TZ, that is essential for the successful acclimation of the entire maize root to oxygen deprivation.[51]

A number of experimental data globally indicates that the transition zone of the root may be considered as a sort of sensory center, enabling the root apex to continuously monitor environment parameters and to trigger appropriate responses.[51-63] Future studies will be needed to deepen the role of this unique root zone in translating the external stimuli in motoric responses.

Nitrate Affects Root Elongation through NO-Elicited Actions

Recently nitric oxide (NO) was proposed to be involved in the regulation of the nitrate-dependent primary root growth.[41] The authors showed that high nitrate supply may reduce IAA levels and subsequently inhibits NO synthase activity, leading to a decrease in the endogenous NO level, which serves as a trigger to elicit nitrate-dependent root growth. A regulatory role for NO in the inhibition of primary root growth has also been suggested in tomato[64] and *Arabidopsis*.[65,66]

Furthermore, a recent study performed in maize provided evidences that NO is produced by nitrate reductase (NR) as an early response to nitrate supply and that the coordinated induction of non-symbiotic hemoglobins (nsHbs) could finely regulate the NO steady-state.[67,68] Both nitric oxide biosynthesis and gene regulation were preferentially accomplished by cells of the transition zone of roots, which would seem the most nitrate responsive portion of maize root.[68] NsHbs play important roles in plant physiology by regulating a number of downstream physiological events involved in plant developmental processes and stress responses, also interacting with many hormonal signaling (for a review see refs 69,70). They catalyze the conversion of nitric oxide to nitrate, contributing to the control of nitric oxide homeostasis in plant cells. They should be considered to be as important as NO generation in regulating *in planta* NO signaling.[70]

Moreover, in this same study,[68] a stimulatory effect of a low concentration of nitrate (1 mM) on root elongation after 1–2 days of treatment was measured in very young seedlings. Nevertheless, when an inhibitor of nitrate reductase activity (tungstate) or a nitric oxide scavenger (cPTIO) were supplied

together with nitrate, no effects on root elongation were observed. On the contrary the treatment of nitrate-depleted roots with a low concentration (10 μM) of a nitric oxide donor (SNP) stimulated root elongation to an extent similar to that measured after nitrate supply. These results strongly suggest that the mechanism through which nitrate affects root elongation is dependent on nitric oxide, as also observed by Zhao et al.[41] even if these authors found some different and in some way opposite results. This apparently contradictory finding could derive from the very different experimental plans and growth conditions utilized in these 2 works, making difficult to compare results obtained. Furthermore, our unpublished results suggest that nitrate is able to affect root elongation in a contrasting mode according to its concentration, acting as a stimulatory signal for concentrations equal or below 1 mM, and as a negative regulator at higher concentrations, suggesting the existence of a multifaceted concentration/time-dependent mechanism of regulation of root growth by nitrate availability.

NO is considered a key regulator of plant developmental processes and defense (for a reviews see refs 70–74), although the mechanism and direct targets of NO action remain largely unknown (for a review see ref. 75 and references therein).

In the case of NO-dependent nitrate regulation of root elongation, the downstream events triggering the root to elongate have still to be identified. Cytoskeletal proteins seem to represent a highly probable molecular target for NO signal[76-78] and accumulating evidences place NO among the key elements in the control of a number of cytoskeleton-mediated processes in plants, such as root growth and development,[79] guard cell dynamic,[80] vesicle trafficking,[76] pollen,[81] and root hair tip growth,[82] or gravitropic bending.[83] In particular, Kasprowicz et al.[76] demonstrated that the actin-dependent endocytosis and organization of the actin cytoskeleton are modulated by NO levels in maize root apices, according to cell-type and developmental stage with the most remarkable effects noticed at level of the transition zone. Thus, the involvement of cytoskeletal rearrangements in the NO-mediated nitrate regulation of primary root elongation is highly conceivable.

Moreover, since NO and auxin act synergically to control diverse aspects of root biology (for a review see Freschi et al.[84]) and lateral root development in response to nitrate is strongly auxin dependent,[85] a role of NO as a coordinator of nitrate and auxin signaling to control the overall root response to the anion cannot be excluded. The involvement of nitric oxide homeostasis control in the root elongation response to nitrate[68] adds a novel component to the complicated puzzle of the root adaptation to nitrate fluctuations in soil (**Fig. 1**). Furthermore, the prominent role of the maize transition zone in the accomplishment of this sensing pathway widens the range of signal/molecules which are sensed and decoded by this particular region of root, which seems to transversally operate in translating a large number of endogenous and exogenous clues in motoric behavior.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

This research was supported by ex-60% 2011–2012–2013 Università di Padova.

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