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INVITED REVIEW

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# Integration of reactive oxygen species and nutrient signalling to shape root system architecture

Łukasz P. Tarkowski[1] | Santiago Signorelli[2,3] | Michael J. Considine[2,4] | Françoise Montrichard[1]

[1]Univ Angers, Institut Agro, INRAE, IRHS, SFR QUASAV, Angers, France

[2]Australian Research Council Centre of Excellence in Plant Energy Biology, School of Molecular Sciences, University of Western Australia, Perth, Western Australia, Australia

[3]Food and Plant Biology group, Departamento de Biología Vegetal, Facultad de Agronomía, Universidad de la República, Montevideo, Uruguay

[4]Department of Primary Industries and Regional Development, Perth, Western Australia, Australia

**Correspondence**
Łukasz P. Tarkowski, Univ Angers, Institut Agro, INRAE, IRHS, SFR QUASAV, F-49000 Angers, France.
Email: Lukasz.tarkowski@inrae.fr

## Abstract

Yield losses due to nutrient deficiency are estimated as the primary cause of the yield gap worldwide. Understanding how plant roots perceive external nutrient status and elaborate morphological adaptations in response to it is necessary to develop reliable strategies to increase crop yield. In the last decade, reactive oxygen species (ROS) were shown to be key players of the mechanisms underlying root responses to nutrient limitation. ROS contribute in multiple ways to shape the root system in response to nutritional cues, both as direct effectors acting on cell wall architecture and as second messengers in signalling pathways. Here, we review the mutual interconnections existing between perception and signalling of the most common forms of the major macronutrients (nitrogen, phosphorus and potassium), and ROS in shaping plant root system architecture. We discuss recent advances in dissecting the integration of these elements and their impact on morphological traits of the root system, highlighting the functional ductility of ROS and enzymes implied in ROS metabolism, such as class III peroxidases.

**KEYWORDS**
class III peroxidase, nitrate, phosphate, potassium, root development, ROS

## 1 | INTRODUCTION

The root system is often overlooked as the front line in the battle to increase crop yield or resistance to stress. Drought, heavy metal, salinity, waterlogging and soil-borne pests are a few examples of extremely relevant challenges in both agriculture and ecology contexts. Nutrient limitation, however, is among the most important challenges, particularly as arable land is increasingly scarce, resulting in a need to expand the environmental competency of crops beyond their present limitations. One of the major levers to improve nutrient acquisition is the plasticity of root system architecture. Reactive oxygen species (ROS) and reduction/oxidation (redox) processes are acknowledged as important enablers of root system plasticity, however, their interactions with nutrient signalling in this context have received little attention. Another major influence on nutrient acquisition, the capacity of nutrient transporters, has been recently reviewed (Yadav et al., 2021) and will not be considered here.

Following germination, root growth through apical cell division and elongation is driven by primary tropic cues, notably gravity, water availability and physical pressure or touch (Muthert et al., 2020). As the root system develops, it encounters a patchy nutrient distribution, influenced by organic input and microbial decomposition (Hodge, 2004; Morris et al., 2017). Plants have therefore evolved nutrient sensing (Gojon et al., 2009; Nath & Tuteja, 2016) to enable root function to adapt to

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heterogeneity by modifying the direction of growth, branching, surface area and branch angle. Other cues, however, are also heterogenous in space and time, including water, oxygen and physical pressure (Considine et al., 2017; Dietrich, 2018). ROS and redox signalling are a common feature of plant responses to these cues, and this enables environmental complexity to be integrated effectively, resulting in an optimal root system architecture (Eljebbawi et al., 2021). The role of phytohormones in this calibration of form is also considerable, but has previously received attention (Sharma et al., 2021; Takahashi et al., 2009), and will not be considered in detail here.

This review highlights the interactions between ROS and nutrient perception in shaping root architecture. We focus on the three most well-studied macronutrients, namely nitrogen (N), phosphorus (P), and potassium (K), also known as the NPK triad, by focusing on their most assimilated forms by roots: nitrate ($NO_3^-$), inorganic phosphate (Pi), and potassium cation ($K^+$). We attempt to describe a framework based on recent research advances, where root response to nutrient scarcity is mediated by changes in ROS signalling and metabolism. For detailed overviews of the discrete roles of ROS and nutrients in root plasticity, the reader is referred to other reviews (Eljebbawi et al., 2021; Huang & Zhang, 2020; Mase & Tsukagoshi, 2021; Shahzad & Amtmann, 2017; Sustr et al., 2019; Undurraga et al., 2017).

## 2 | ROS METABOLISM AND SIGNALLING PLAY MULTIPLE ROLES IN ROOT DEVELOPMENT

ROS have long been viewed as toxic compounds, generated as byproducts of metabolism; their overaccumulation leads to oxidative damage and cell disfunction (Desikan et al., 2005; Farooq et al., 2019). Antioxidants such as glutathione and ascorbate, which are the most abundant soluble antioxidants, together with the operation of redox metabolism, enables recycling and the precise control of ROS abundance in space and time. Therefore, ROS are increasingly becoming recognised as having important physiological roles in plant development and stress response, notably when they are produced as primary products in apoplast and cell wall (Mittler, 2017). For example, ROS gradients were shown to control root and root hair elongation (Chu et al., 2021; Foreman et al., 2003; Liszkay et al., 2004; Mangano et al., 2017; Tognetti et al., 2017; Trevisan et al., 2019; Tsukagoshi et al., 2010). Three main ROS produced in the apoplast, superoxide anion radical ($O_2^{\cdot-}$), hydroxyl radical (·OH), and hydrogen peroxide ($H_2O_2$), participate in these processes. In this review, we consider ROS functions in root development as functioning in one of two primary roles: direct effects and signalling (indirect effects) (Figure 1).

### 2.1 | Enzymes involved in root ROS metabolism in the apoplast

In the apoplast, ROS are produced and/or processed principally by NADPH oxidases, superoxide dismutases (SODs) and class III peroxidases (PODs). NADPH oxidases form a small family of plasma membrane proteins found in plants (10 members in Arabidopsis) which reduce $O_2$ to $O_2^{\cdot-}$ in the apoplast using cytosolic NADPH as an electron donor (Chapman et al., 2019; Sagi & Fluhr, 2001). They are homologues of the respiratory burst oxidases found in animals and for this reason, they are also named respiratory burst oxidase homologues (RBOHs). Such enzymes are known to cover important roles in the physiology of all the parts of the root system, especially in lateral roots and root hairs. Early studies in the Arabidopsis mutant *rhd2* (*root hair-defective mutant 2*), inactive for the RBOH isoform C (RBOHC), showed that RBOHC activity is needed for root hair development where it controls the activation of $Ca^{2+}$ channels (Foreman et al., 2003). RBOH activity is also responsible for the formation of ROS gradients that drive directional growth in root

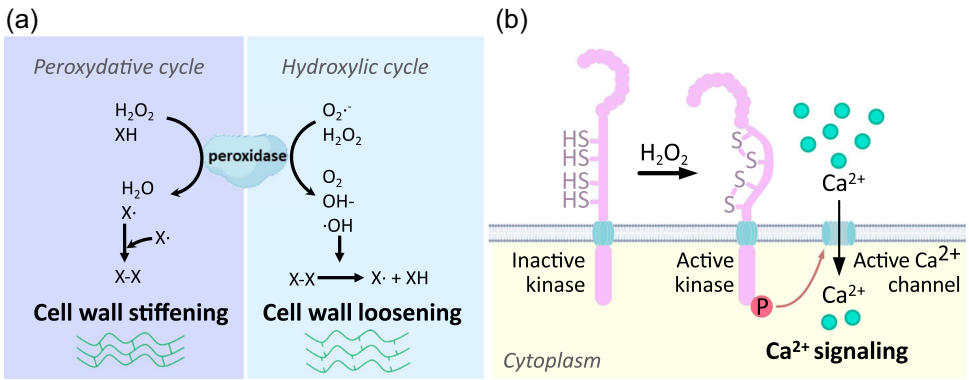



**FIGURE 1** Reactive oxygen species (ROS) can affect root development in direct and indirect ways. (a) Direct mode of action: class III peroxidases can directly act on cell wall polymers (X) through their peroxidative and hydroxylic cycles. In the first case, electron transfer from $H_2O_2$ to X favours polymer crosslinking and thus cell wall stiffening, while in the second case hydroxyl radicals (·OH) can break cell wall polymer crosslinks and result in cell wall loosening. (b) Indirect mode of action: the case of the HPCA1 receptor illustrates the role of ROS as signalling molecules. In the presence of $H_2O_2$, two pairs of Cys located on the extracellular domain of HPCA1 are oxidised, triggering a conformational change that activates the intracellular kinase domain. This leads to the phosphorylation of adjacent $Ca^{2+}$ channels and a rapid increase of $[Ca^{2+}]_{cytosol}$, resulting in the activation of $Ca^{2+}$-dependent signalling pathways. [Color figure can be viewed at wileyonlinelibrary.com]

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hairs (E.-J. Kim et al., 2019; Nestler et al., 2014; Takeda et al., 2008). In lateral roots, ROS generated by RBOHs are required in the emergence stage, where they remodel the tissue layers lying above the lateral root primordia dome (Arthikala & Quinto, 2018; Orman-Ligeza et al., 2016). In the primary root of *Medicago truncatula*, RBOH-dependent ROS increase was shown to trigger cell elongation, while in Arabidopsis primary roots ROS generated through AtRBOHD/F are known to be required for ABA-dependent growth inhibition (Jiao et al., 2013; Kwak et al., 2003; Zhang et al., 2014). RBOH expression in a cell can be induced by RBOH activity in neighbouring cells, resulting in the propagation of the ROS signal to act as a systemic response. This phenomenon has been denominated the 'ROS wave' (Mittler et al., 2011).

The SOD family comprises a small number of isoforms, divided into Mn-SOD, Fe-SOD, and Cu/Zn-SOD based on the ion used as cofactor. SOD catalyzes the dismutation of the majority of apoplastic $O_2^{\cdot-}$ to $H_2O_2$; a minority of dismutation occurs spontaneously (Podgórska et al., 2017). Recently, MSD2, a protein considered to belong to the Mn-SOD family, was confirmed to act as an Mn-SOD but unlike most Mn-SOD which have mitochondrial localisation, it accumulates in the apoplast of roots of Arabidopsis seedlings (H. Chen et al., 2022). The roots of Arabidopsis seedlings lacking MSD2 showed an altered skotomorphogenesis, such that the onset of root hair growth was delayed, and their location was closer to the root tip than wild type. To date, however, this is the only report of the function of apoplastic SOD in root development; other studies have documented functions for mitochondrial and plastid SOD (Dvořák et al., 2021; Morgan et al., 2008).

Class III PODs form a large family of isoenzymes comprising 73 members in Arabidopsis (Lüthje & Martinez-Cortes, 2018). They are only present in plants and are in large part addressed to the plasma membrane or cell wall. They can perform different activities such as an oxidative activity producing $O_2^{\cdot-}$ at the expense of NADH, a hydroxylic activity producing $^{\cdot}OH$ from $O_2^{\cdot-}$ and $H_2O_2$, and a peroxidative activity eliminating $H_2O_2$ using substrates such as cell wall phenolic compounds or auxin (S. Chen & Schopfer, 1999; Passardi et al., 2005; Šukalović et al., 2005; Veljović Jovanović et al., 2018). Although class III PODs can catalyse all these reactions in vitro (Passardi et al., 2004), their activities in planta might be specialised, depending on spatio-temporal expression of the genes, specificity of the enzymes for the substrates, availability of substrates and regulation by factors such as pH alkalinization, calcium binding, glycosylation or phosphorylation (Cosio & Dunand, 2009; Felle, 2001; Francoz et al., 2015; Mangano et al., 2016; Shigeto & Tsutsumi, 2016). This versatility might be the reason for maintaining such a large family of functional genes, which can be used in multiple ways in a plethora of different stress responses and developmental processes (Eljebbawi et al., 2021; Passardi et al., 2005). POD isoforms present in the root tip were shown to play a crucial role in the control of root ROS patterns and its gradients in the root tip, which in turn determine the transition from a zone of proliferation to a zone of elongation and differentiation (Tsukagoshi et al., 2010). These PODs are under the control of the helix-loop-helix transcription factor UPBEAT1, which is mostly expressed in the transition and elongation zones (Trevisan et al., 2019; Tsukagoshi et al., 2010). Likewise, specific PODs (Arabidopsis PRX01, PRX44, and PRX73) were suggested to be involved in the ROS-mediated assembly of extension networks, which are important for root hair development in Arabidopsis (Marzol et al., 2022).

## 2.2 | ROS-dependent control of root growth through direct modification of the cell wall

ROS-dependent control of root growth is exerted through a direct modification of the cell wall. ROS accumulation in primary root tips is a critical feature to determine growth rates (Dunand et al., 2007; Liszkay et al., 2004; Trevisan et al., 2019; Tsukagoshi et al., 2010; Zang et al., 2020). ROS form concentration gradients to either promote growth through cell division in the meristem zone ($O_2^{\cdot-}$) and cell elongation in the elongation zone ($^{\cdot}OH$) through polymer breaking and cell wall loosening or, in contrast, restrict growth in the differentiation zone ($H_2O_2$) through polymer cross-linking and cell wall stiffening (Dunand et al., 2007; Liszkay et al., 2004; Tsukagoshi et al., 2010) (Figure 2). Other processes that seem to require direct ROS action include mature tissue differentiation mechanisms such as xylem differentiation and Casparian strip formation (Fernández-Marcos et al., 2017; Hoffmann et al., 2020; Lee et al., 2013; Mangano et al., 2017).

## 2.3 | ROS can act as messengers in signalling pathways involved in root development

One can imagine that when ROS accumulate above a given threshold in the apoplast of the root tip, they can enter the adjacent cells and affect the redox poise of the cytoplasm, oxidising the soluble antioxidants glutathione and ascorbate. $H_2O_2$ is a good candidate for this role because it is relatively stable, with a half-life of ~1 ms by comparison with 2–4 μs for $O_2^{\cdot-}$ and $^{\cdot}OH$ (Smirnoff & Arnaud, 2019). Moreover, its small size facilitates passive transport across membranes and through plasmodesmata and aquaporins (Dynowski et al., 2008; Wu et al., 2020). Finally, $H_2O_2$ functions in systemic ROS signalling – the so-called ROS wave mentioned above – where $H_2O_2$ synthesis is propagated from cell to cell, functioning synergistically with $Ca^{2+}$ signalling to trigger acclimation responses (Mittler et al., 2022). The recently identified HYDROGEN-PEROXIDE-INDUCED $CA^{2+}$ INCREASES (HPCA1) protein establishes the functional link between these two small signal molecules (Wu et al., 2020).

Within the cell, catalase is a key enzyme in processing $H_2O_2$. The function of CAT2 is most well-established in photorespiration (Yang et al., 2019), although it is also required to enable orderly β-oxidation during post-germinative growth (Liu et al., 2017). Moreover, CAT2 plays a role in alleviating stress under prolonged iron deficiency. Catalase is Fe-dependent, and under prolonged Fe deficiency, cellular $H_2O_2$ levels are elevated, and root elongation is enhanced (von der Mark et al., 2021). The *cat2-1* mutants show impaired iron

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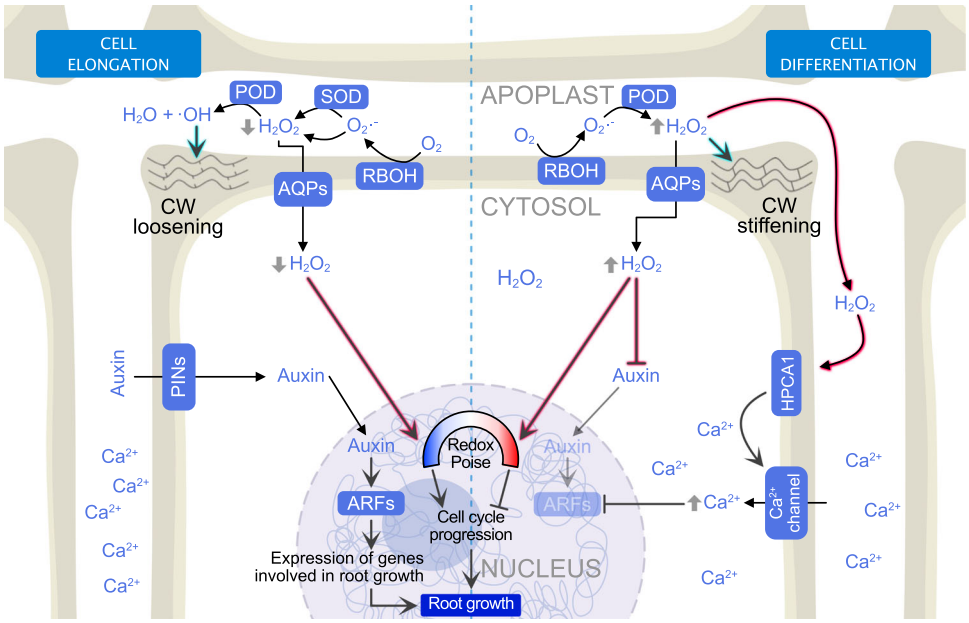



**FIGURE 2** Involvement of reactive oxygen species (ROS) metabolism in root cell elongation and differentiation. The left-hand side of the figure shows the how ROS metabolism is regulated and coordinated with other signals to promote root cell elongation, whereas the right-side of the figure shows the involvement of these molecules in root cell differentiation. Arrows with cyan outer glow indicate a direct function of ROS in cell wall modification, whereas arrows with a magenta outer glow indicate their signalling role through oxidation of specific protein residues to modulate enzymatic functions. AQPs, Aquaporins; ARFs, Auxin response factors; HPCA1, Hydrogen-peroxide-induced $Ca^{2+}$ Increases (a $H_2O_2$ plasma membrane receptor); POD, Peroxidases; R, Respiratory burst oxidase homologue; SOD, Superoxide dismutase. [Color figure can be viewed at wileyonlinelibrary.com]

homoeostasis, although the underlying mechanisms require full elucidation.

The studies of mutants deficient in ascorbate and glutathione have been formative for our understanding of ROS functions in development and abiotic stress (Considine & Foyer, 2014). Mutants severely deficient in glutathione display a defective primary root (Vernoux et al., 2000) and reduced number of lateral roots (Hoang et al., 2021) as well as elevated sensitivity to biotic and abiotic stress (Hoang et al., 2021). Mutants for ascorbate production (*vtc1*, vitamin C defective 1) also have shorter primary root but develop more lateral roots than WT plants. Curiously, other vitamin C defective mutants (*vtc2-4* and *vtc5-2*) did not display differences in terms of primary root but exhibited a reduced number of secondary roots in control conditions. However, under different abiotic stress conditions the vitamin C defective mutants (*vtc2-4* and *vtc5-2*) develop much more secondary roots than WT plants (Hoang et al., 2021). Together, these data suggest that both ascorbate and glutathione participate in the plasticity of the root architecture system, both in control and stress conditions. Moreover, in two independent studies, greater oxidation of glutathione and ascorbate was shown to induce G1 arrest in cells of the quiescent centre in the root apical meristem (Considine & Foyer, 2014; Velappan et al., 2017), suggesting that glutathione- and ascorbate-dependent regulation of cytosolic ROS levels is required for a correct root system development (De Simone et al., 2017).

Recent research in Arabidopsis showed that not only $H_2O_2$ but also $O_2^{\cdot-}$ have a critical role in root apical meristem maintenance as they act as second messengers downstream of the signalling initiated by the perception of the peptide hormone Root Meristem Growth factor 1 (RGF1). This signalling pathway modulates the $O_2^{\cdot-}/H_2O_2$ balance across the root tip, and increased $O_2^{\cdot-}$ levels were shown to increase the stability of PLETHORA2 proteins, a master regulators of root development (Yamada et al., 2020).

## 2.4 | ROS signal transduction through protein oxidation

ROS accumulated inside the cells not only oxidise glutathione and ascorbate but also macromolecules such as proteins. The sulphurs present in exposed Cys and Met residues of many proteins are susceptible to nucleophilic attack, resulting in posttranslational redox modifications crucial for various cellular functions (Mittler et al., 2022; Mock & Dietz, 2016). Such modification can lead to loss or gain of protein function and has been proposed to play a role in the transduction of $H_2O_2$ signals. This was first demonstrated in yeast with a glutathione peroxidase (GPX) involved in the activation of a transcription factor that results in protection of the yeast from oxidative damage (Delaunay et al., 2002). GPXs are a large family of non-heme peroxidases with different subcellular localisations that use either the thiol group of thioredoxins or glutathione as an electron acceptor to reduce $H_2O_2$ and organic peroxides (Bela et al., 2022). In plants, GPXs playing a role in lateral root development were identified (Passaia et al., 2014). Whether

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their role is linked to transduction of an $H_2O_2$ signal remains to be determined. $H_2O_2$ signalling through protein redox modification was nevertheless demonstrated in plants for the HPCA1 sensor, a leucine rich repeat receptor kinase (Wu et al., 2020). Once its reactive Cys residues are oxidised by apoplastic $H_2O_2$, it induces a $Ca^{2+}$ influx, providing the molecular link between observations reporting a concomitant apoplastic ROS production and $Ca^{2+}$-mediated responses (Gilroy et al., 2016; M. J. Kim et al., 2010; Mori & Schroeder, 2004; Wu et al., 2020). Given the capacity of $Ca^{2+}$ to modulate several signalling pathways, the discovery of HPCA1 provides direct evidence of how apoplastic $H_2O_2$ and redox status can determine the fate of diverse biological processes, connecting RBOH- and POD-dependent apoplastic ROS accumulation to intracellular downstream responses (Figure 2).

Protein oxidation may be reversible following reduction back to the native state through the action of redoxins, proteins susceptible to redox posttranslational modifications thanks to the highly reactive thiol groups present in exposed Cys residues (Meyer et al., 2008). Based on the cofactor used as reducing agent, redoxins can be classified as thioredoxins (TRXs) (NADPH as reducing agent), glutaredoxins (GRXs) (glutathione as reducing agent), and peroxiredoxins (PRXs, as they lack a cofactor they require an external electron donor, such as TRXs or GRXs, for regeneration after each catalytic cycle). The redoxin family is well-known in plants (Montrichard et al., 2009), but available information about the isoforms involved in root development is limited. However, four GRXs (S3, S4, S5 and S8) involved in the control of primary root growth were identified in Arabidopsis in a transcriptomic analysis of shoot response to N nutrition (Patterson et al., 2016; see Section 3.1). In this study, the inactivation by RNAi silencing of all four corresponding genes, which are similar and in tandem, led to mutant plants with increased primary root length. Later, other GRXs (of the ROXY subclass) involved in root hair elongation were identified (Jung et al., 2018). Regarding the roles of TRXs in root development, not much is known to date, although two TRX isoforms of Arabidopsis were suggested to be required for correct activity of the root apical meristem (Reichheld et al., 2007).

The roles of ROS in root development have been recently reviewed (Eljebbawi et al., 2021; Mase & Tsukagoshi, 2021; Zhou et al., 2020). In the following sections, we focus specifically on their roles in regulating the root system architecture in response to nutrient stress.

## 3 | ROS AND NUTRIENT STRESS

### 3.1 | $NO_3^-$ deficiency and ROS homoeostasis: An intricate relation

N deficiency was first shown to induce ROS accumulation in a localised manner in the root hair extremities of Arabidopsis (Shin et al., 2005). Changes in ROS accumulation linked to $NO_3^-$ availability were later observed in the primary root tips of maize (*Zea mays*) and *M. truncatula*. In maize, $NO_3^-$ deficiency was shown to activate a signalling pathway that stimulates primary root elongation by inducing POD-dependent $H_2O_2$ accumulation, which promotes cell elongation and differentiation (Trevisan et al., 2019). On the other hand, an excess of $NO_3^-$ reduced $H_2O_2$ levels but increased $O_2^{\cdot-}$ levels. Thus, it seems that the balance between these molecules might be key in regulating root growth in response to $NO_3^-$ (Trevisan et al., 2019). The authors found a maize orthologue of AtUPBEAT1 transcription factor to be responsible for regulating ROS levels by repressing the expression of a POD gene (*Zm00001d024119*) in a similar fashion to what was described in Arabidopsis, suggesting the existence of an evolutionarily conserved signalling module common to both monocots and eudicots (Trevisan et al., 2019; Tsukagoshi et al., 2010). Accordingly, in *M. truncatula*, the orthologue of *AtUPBEAT1*, *MtUPBEAT1*, was recently found to be downregulated in response to 5 mM $NO_3^-$ treatment (Zang et al., 2022).

In *M. truncatula*, the $NO_3^-$ transporter MtNPF1.7 controls ROS homoeostasis in the primary root tip and promote cell elongation through an increased RBOH activity (Zhang et al., 2014). A link between ROS accumulation and $NO_3^-$ availability was proposed although conclusive evidence was lacking. The link was made later by showing that $NO_3^-$ deficiency increases ROS accumulation in the primary root tip of *M. truncatula* seedlings, following changes in POD activities levels (Figure 3) (Zang et al., 2020). In the presence of 5 mM $NO_3^-$, a net decrease in $H_2O_2$ and ·OH was notably correlated with an increase in POD peroxidative activity (which eliminates $H_2O_2$) and a decrease in POD hydroxylic activity, which produces ·OH. Interestingly, no change in ROS accumulation or POD activity was observed in the primary root tip of the mutant *npf6.8* deficient in the $NO_3^-$ transporter MtNPF6.8 that has lost the sensitivity to $NO_3^-$ (Zang et al., 2022). It is noteworthy that such a mechanism does not occur in lateral roots, in which growth rate is enhanced in the presence of $NO_3^-$. In Arabidopsis, enzymes of the GPX family were found to be required for the correct development of lateral root primordia (Passaia et al., 2014). Thus, it remains possible that the GPX-dependent control of $[H_2O_2]_{cytosol}$ during lateral root development has to be more stringent compared to the control of $[H_2O_2]_{apoplast}$, which on the other hand appears to be mostly delegated to PODs and is a major factor in primary root development.

The comparison of the results obtained in maize and *M. truncatula* highlights some differences and indicates that the relation ROS-$NO_3^-$ may be rather species-specific (Figure 4). However, it reveals a central role played by $H_2O_2$ in the control of the root growth by $NO_3^-$ that was further supported by experiments in which $H_2O_2$ concentration was manipulated during *M. truncatula* root growth. In this work, exogenous $H_2O_2$ was shown to completely abolish the $NO_3^-$ effect on both the primary root growth and the lateral roots while KI, an $H_2O_2$ scavenger, mimicked $NO_3^-$ effects (Zang et al., 2020).

The *GRX S3*, *S4*, *S5* and *S8* genes identified in Arabidopsis are induced in the shoot by a $NO_3^-$ signalling pathway mediated by cytokinins to inhibit primary root growth (Patterson et al., 2016). To explain this long-distance effect, the authors proposed a model where the products of the genes were transported in the phloem to the primary root

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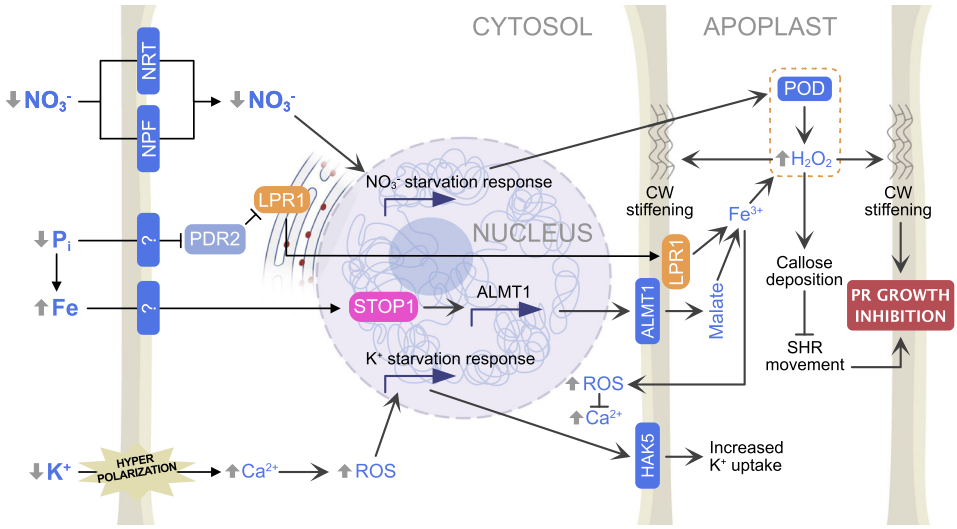



**FIGURE 3** Signalling effect of nitrate, phosphate, and potassium on primary root growth. $NO_3^-$ and Pi deficit induce primary root growth inhibition, through apoplastic $H_2O_2$ accumulation and callose deposition. Moreover, $Ca^{2+}$ and reactive oxygen species (ROS) signalling participates in the increase of potassium uptake under potassium deficit conditions. ALMT1, Aluminium-activated malate transporter 1; HAK5, High affinity $K^+$ transporter; LPR1, Low phosphate root1; NPF, NRT1/PTR family; NRT, Nitrate transporter; PDR2, Phosphate deficiency response 2; PHR, Phosphate starvation response; PR, primary root; SHR, Short root; STOP1, Sensitive to proton rhizotoxicity 1. For further discussion, see text. [Color figure can be viewed at wileyonlinelibrary.com]

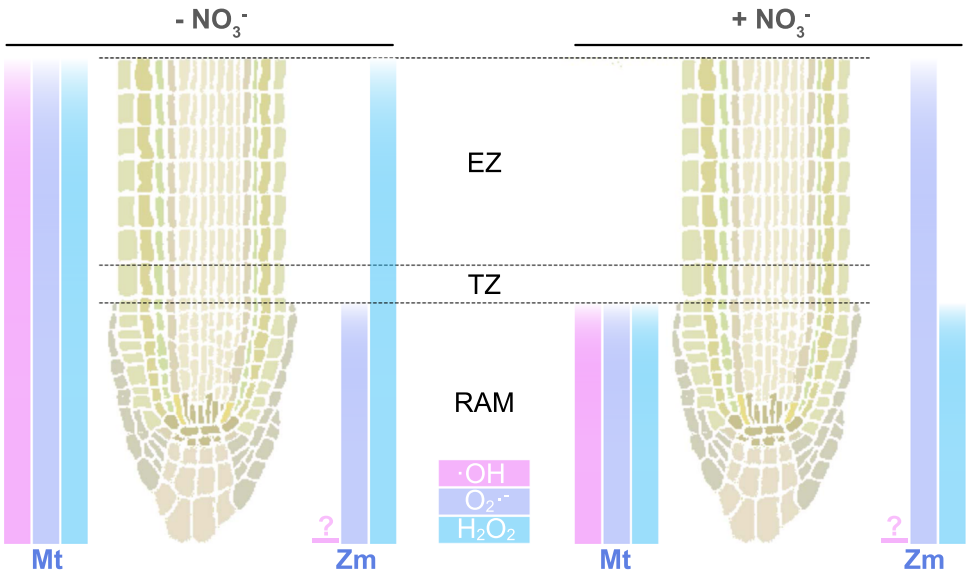



**FIGURE 4** Effects of $NO_3^-$ supply on reactive oxygen species (ROS) accumulation in root tips of *Medicago truncatula* and maize. The left panel presents an absence of $NO_3^-$ supply to roots, while the right panel shows a $NO_3^-$-sufficient condition. The right half of each root represents data from maize (Zm), left part data from *M. truncatula*. Bars indicate the extent of accumulation of each ROS in the root in relation to species and $NO_3^-$ status. Note that data for ·OH quantification are not available for maize. Data elaborated from Trevisan et al. (2019), Zang et al. (2020). EZ, elongation zone; RAM, Root apical meristem; TZ, transition zone. [Color figure can be viewed at wileyonlinelibrary.com]

to both reduce the growth and induce an expression of the $NO_3^-$ transporter gene *AtNRT2.1* when $NO_3^-$ is present. Such a hypothesis was latter supported by the work of the Matsubayashi group (Ohkubo et al., 2017; Ota et al., 2020). The *GRX* genes identified in these studies were overexpressed in the shoot in response to CEP (C-terminally encoded peptide), a root-to shoot peptide originating from the N-starved roots, and as a result were named C-terminally encoded peptide downstream 1 (CEPD1) (Ota et al., 2020).

Two *ROXY* GRX genes were shown to be oppositely regulated, in a manner that functionally influenced the growth response to $NO_3^-$ availability. *AtROXY9* was upregulated while *AtROXY15* was downregulated in response to $NO_3^-$ starvation in Arabidopsis

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seedlings. Overexpression of *AtROXY9* enhanced the length of root hairs as compared to the wild type, while seedlings over-expressing *AtROXY15* showed shorter root hairs. This suggests that the regulation of GRX expression is crucial to modulate root hair growth in both $NO_3^-$-deficient and sufficient conditions (Jung et al., 2018).

More recent research from Arabidopsis showed that $NO_3^-$ starvation represses the expression of several GARP (Golden2, ARR-B, Psr1) family transcription factor genes, which are responsible for keeping intracellular ROS levels low by positively regulating the expression of different redoxin genes and repressing *RBOHC* expression (Safi et al., 2021). The resulting ROS accumulation is required to regulate a large subset of genes involved in the $NO_3^-$ starvation response, including several high-affinity $NO_3^-$ transporters (Safi et al., 2021). Besides GARP transcription factors, the HOMOLOGUE OF BRASSINOSTEROID ENHANCED EXPRESSION2 INTERACTING WITH IBH1 (HBI1) transcription factor was recently highlighted as another key regulator of ROS levels in response to $NO_3^-$ availability, in both roots and shoots of Arabidopsis (Chu et al., 2021). Here, the authors showed that high environmental $NO_3^-$ levels induce *HBI1* expression, which in turn promotes the expression of several PODs genes and *CAT2* (a catalase gene), resulting in low ROS cellular levels (Chu et al., 2021). The combination of these findings with the previously mentioned research on the roles of POD in primary root development points to a scenario where ROS act both as signal and effectors in response to $NO_3^-$ availability depending on spatio-temporal variables.

## 3.2 | ROS and Fe availability are determinant in Pi deficiency responses

Pi availability is one of the most limiting nutritional cues for plant growth. Therefore, plants have developed sophisticated sensing and signalling mechanisms to optimise Pi uptake as a function of its external concentrations (Chien et al., 2018). ROS have been known to be involved in Pi signalling pathways for almost two decades, when Pi deficiency was shown to induce ROS production in the cortex of primary roots but not in the tips of Arabidopsis, leading to the hypothesis that ROS are involved in Pi deficiency signalling (Shin et al., 2005). Further research showed that such ROS accumulation has a negative effect on primary root growth and stimulates lateral root growth, according to a model of the root ideotype optimised for Pi acquisition from the topsoil (Tyburski et al., 2009, 2010; York et al., 2013).

Although the initial step in Pi sensing is yet to be uncovered, it is known that one of the earliest signalling steps is the loss of the interaction between the nuclear proteins SPX (SYG/PHO81/XPR1 domain protein) and PHR (phosphate starvation) transcription factor, which is then released and activated (Puga et al., 2014). This pathway is known to govern Pi starvation responses at the systemic level. At the local level, studies on Arabidopsis roots indicated that two pathways appear to control Pi deficiency-dependent primary root growth inhibition: the PDR2-LPR1/2 and the STOP1-ALMT1 modules (Crombez et al., 2019). In the first case, low extracellular Pi levels triggers the relocation of the ER localised ferroxidase low phosphate root1 (LPR1) to the cell wall where it triggers Fe accumulation and promotes $H_2O_2$ accumulation and callose deposition (Figure 3, Müller et al., 2015). Not much is known about the elements upstream of LPR1, besides that it is under negative genetic control of the ER-resident ATPase PDR2 (phosphate deficiency response 2) (Figure 3, Ticconi et al., 2009).

In parallel with this pathway, a high extracellular Fe/Pi ratio, typical of low Pi conditions, post-transcriptionally activates the transcription factor STOP1 (sensitive to proton toxicity1) which triggers an increase in apoplastic malate concentration by upregulating the gene expression of the ALMT1 transporter (aluminium-activated malate transporter 1) (Figure 3). Such malate accumulation was shown to further increase apoplastic $Fe^{2+}$ availability, which ultimately triggers apoplastic ROS accumulation and callose deposition (Balzergue et al., 2017; Godon et al., 2019). While callose deposition around plasmodesmata limits the movement of the SHORTROOT transcription factor, a master regulator of primary root development (Salvi et al., 2018), increased apoplastic $H_2O_2$ sustain the peroxidative cycle of PODs, resulting in increased cell wall stiffening (Balzergue et al., 2017; Müller et al., 2015). Both events ultimately inhibit primary root elongation (Figure 3). Thus, it appears that POD activity is a one of the major determinants of Pi deficiency-induced inhibition of primary root growth. Accordingly, proteomic and transcriptomic data from Arabidopsis primary root tips revealed that Pi starvation modulates the expression of about 30 PODs (Hoehenwarter et al., 2016). Taken together with the data discussed in the previous paragraph, a scenario is emerging whereby PODs act as central actors in root system architecture plasticity in response to both Pi and $NO_3^-$ starvation. This might not come as a surprise given that several points of convergence between Pi and $NO_3^-$ signalling are already known (Hu et al., 2019; Medici et al., 2019; Pueyo et al., 2021).

In addition to the modulation of apoplastic ROS, intracellular ROS accumulation was shown to take place as a consequence of increased $Fe^{2+}$ availability following Pi starvation in the Arabidopsis primary root (Matthus et al., 2019), although the biological significance of this event remains to be elucidated. It would be interesting to test whether GPXs are involved in this process, as is the case during $NO_3^-$ starvation.

Although modulation of primary and lateral root growth is required to increase Pi acquisition from the topsoil, possibly the most influential evolutionary adaptation of roots to cope with Pi deficiency was the increase in root hair length and density (López-Bucio et al., 2002; York et al., 2013). Such an adaptation allows a more efficient soil acidification and thus increased Pi solubilisation. In this context, research in Arabidopsis showed that Proline-rich Extensin-like Receptor Kinase 13 (PERK13) is involved in Pi sensing and that loss-of-function mutants of *PERK13* have altered root hair development in response to Pi deficiency. Both gain-of-function and loss-of-function *PERK13* mutant lines showed increased ROS

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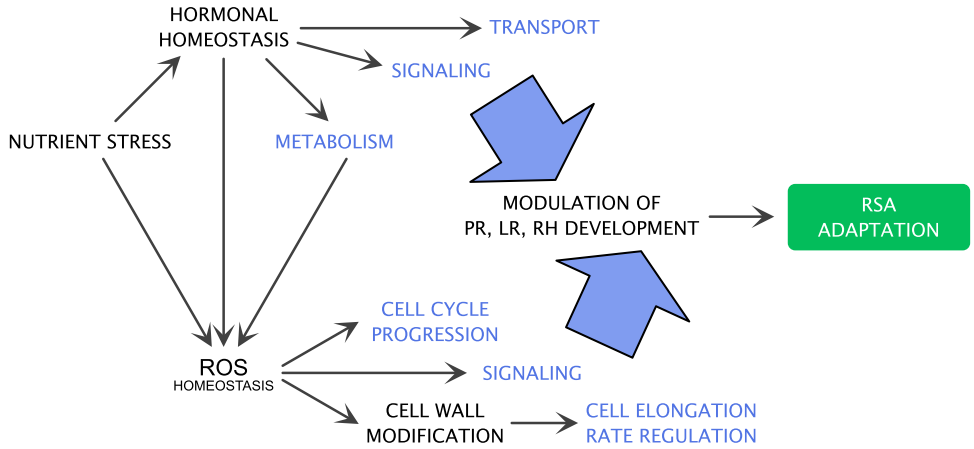



**FIGURE 5** Schematic representation of the main pathways downstream of nutrient stress that modulate root system architecture. Nutrient stress induces changes in the hormonal homoeostasis, including their metabolism, transport, and signalling which in turn modulate primary root, lateral root and root hair development. Both nutrient stress and hormonal metabolism modulate reactive oxygen species (ROS) homoeostasis which affects cell cycle progression and cell wall composition. These events together with ROS signalling also modulate the development of the primary root, lateral roots, and root hairs. [Color figure can be viewed at wileyonlinelibrary.com]

accumulation in root hairs under Pi deficiency compared to WT lines. These observations suggest that PERK13 controls ROS levels, and thus growth rate, in root hairs in response to Pi deficiency (Xue et al., 2021). It remains to be determined which ROS-producing enzymes are the downstream targets of this kinase.

### 3.3 | ROS functions in $K^+$ deficiency responses

Compared to $NO_3^-$ and Pi, our current knowledge about root responses to $K^+$ deficiency is relatively limited. Recent research efforts are aiming to fill this gap (Sustr et al., 2019; Wang et al., 2021). Nevertheless, an important role for ROS in root system architecture response to $K^+$ deficiency has been known for some time. The activity of RBOHs are known to be required to induce the expression of genes involved in the $K^+$ deficiency response, such as genes encoding high-affinity $K^+$ transporters in the primary root of Arabidopsis (Shin & Schachtman, 2004). When RBOH activity was inhibited by DPI, exogenous application of $H_2O_2$ was able to restore the expression levels of genes coding for high-affinity $K^+$ transporters (Shin & Schachtman, 2004), highlighting the importance of extracellular ROS production in early response to $K^+$ deficiency. Recent research in *Nicotiana tabacum* roots subjected to $K^+$ deficiency showed that such ROS accumulation is downstream of $Ca^{2+}$ signalling (Wang et al., 2021), although it remains to be determined how this increase in cytosolic $Ca^{2+}$ triggers ROS accumulation.

The POD AtRCI3 was also previously shown to be involved in ROS production upon $K^+$ deficiency and to positively regulate the expression of the *AtHAK5* high-affinity transporter gene in Arabidopsis, a master gene of the $K^+$ deficiency response (M. J. Kim et al., 2010). Interestingly, overexpression of *AtRCI3* correlates with increased ROS levels in the primary root, suggesting that the main activity of this POD is linked to ROS generation rather than detoxification.

## 4 | CONCLUSIONS AND PERSPECTIVES

To date, research into the regulators of root system plasticity in response to nutrient availability has mostly focused on hormonal influences. Studies discussed here have highlighted the crucial role of ROS and redox processes in signalling pathways that facilitate or interact with nutrient sensing (Figure 3). ROS and redox signalling act on cellular processes such as cell division and expansion in ways that are dependent on, and independent of, hormone functions. ROS can directly influence hormonal dynamics, as shown in the case of attenuation of auxin signalling through oxidation (Peer et al., 2013) (Figure 5). Conversely, several hormones, such as abscisic acid, auxins, cytokinins, and ethylene are known to influence ROS accumulation in roots. Thus, integrating research on ROS homoeostasis and hormonal signalling in response to nutrient stress is a necessary step to achieve a more comprehensive understanding of root system plasticity, as already suggested by earlier studies (Mangano et al., 2017; Zhang et al., 2014). We suggest that the complex and coordinated interplay between hormones and ROS is the main determinant that constitutes the backbone for signal transduction that allows the root system architecture to respond to nutritional cues, ultimately resulting in modifications of root morphology (Figure 5).

The identification of master regulators situated at the interface of ROS and nutrient signalling pathways will help us achieve a more detailed description of how molecular inputs are converted to morphological outputs in plant roots, potentially revealing powerful targets for crop amelioration. By combining studies on the impact of nutrient deficiency with investigations into spatial and temporal

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changes in ROS dynamics, important mechanistic details can be added to our current knowledge of root responses to nutrient stress. A next step in this process will be to integrate such knowledge with the effect of root microbiota on nutrient acquisition and consider the concerted effect of multiple nutrient stresses. A full consideration of such a multitude of factors will be crucial to generate knowledge that can be applied to crops growing in field conditions.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## ORCID

*Łukasz P. Tarkowski* http://orcid.org/0000-0002-5419-6606
*Santiago Signorelli* http://orcid.org/0000-0002-1854-3164
*Michael J. Considine* http://orcid.org/0000-0002-4468-6820
*Françoise Montrichard* http://orcid.org/0000-0001-8769-0128

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