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Nutritional stress in plants: Understanding sensing and resilience

Since the emergence of the Mineral Nutrition theory during the XIX century (van der Ploeg et al., 1999; Feller et al., 2003), the relevance of mineral plant elements in the life of plants has become well documented. Meanwhile, a progressive number of studies helped to establish that most plants are able to acquire all the elements necessary for growth and development from inorganic sources. Because of the improvement of analytical techniques, a rising corpus of evidence has shown that plants usually incorporate within their tissues many of the elements present in the environments they inhabit. Several works indicate that some of these elements could positively affect plant performance, thus suggesting that during evolution plants have used mineral resources encountered in their habitats helping to ensure their survival and reproductive success. These observations pose important questions on how plants acquire and utilize those elements, which vary greatly in their availability in the soil. One key question refers to the way by which plants perceive fluctuations in elements availability and respond accordingly, and also how they integrate the emerging signals with those coming from the fluctuations of other biotic and abiotic components to yield a unified response, thus impacting the efficiency by which functional plant elements are acquired and utilized. A clear understanding of these issues seems to be critical to develop strategies to ensure the production of grains and pastures for a growing population while minimizing the negative impact of agronomic practices on the environment. In this special issue on Nutritional Stress in Plants, the contributions made by authors from many different countries address some specific topics related to those questions.

1. The roles of functional plant elements in the life of plants

Although the action of either essential and beneficial mineral elements has commonly been ascribed to their impact on nourishing, it seems now clear that several mineral elements that positively influence plant life have further functions. Emerging evidence supports the influence of mineral elements not only related to structural roles or energy transfer, but also with signaling, defense to herbivory as well as in the emergence of, and in the response to, multiple symbiotic and non-symbiotic interactions, which formerly led to the proposal to consider them as functional plant elements instead of nutrients (Santa-María et al., 2023). In this issue, Houmani and Corpas (2024) revised the functionality of a specific set of mineral elements in signaling processes. Particularly, they examined the role of calcium (Ca^{2+}), potassium (K^{+}), magnesium (Mg^{2+}), nitrogen (N), phosphorus (P), and iron (Fe) as components of the signaling machinery, paying special attention to their involvement in the response of plants to stress conditions. By considering several sources of evidence the authors argued that the status of mineral elements in plant tissues must be conceived beyond the deficiency/overabundance paradigm as it constitutes an important signaling component in the response of plants to numerous stress conditions. Among the above-mentioned elements, Ca^{2+} has been shown to play pivotal signaling functions. Noticeably, several processes in which Ca^{2+} acts as a regulatory signal further involve the interaction between Calcineurin B-like proteins (CBLs) and CBL-interacting kinases (CIPKs), being their interaction critical for the homeostasis of several functional elements. In this regard, Amo et al. (2024) examined the role of tomato CIPK23 (SlCIPK23) in the acquisition of sodium (Na^{+}), a non-essential element for most plants that can enhance plant performance in low K^{+} environments. Amo and coworkers observed that the accumulation of Na^{+} occurs through both ammonium (NH_4^{+}) sensitive and NH_4^{+} insensitive pathways, with SlCIPK23 regulating the NH_4^{+} sensitive system. The authors argued that the HKT transporters, early shown to be involved in Na^{+} transport from diluted Na^{+} solutions, may be not the primary targets of action of SlCIPK3, while they also showed that the addition of Na^{+} can revert the anomalous root growth phenotype displayed by mutant *slcipk23* plants.

2. Nitrogen: Sensing and use

An interesting example of a functional plant element is N, which plays interconnected nourishing and signaling roles. Nejamkin et al. (2024) provided a comprehensive review of the role of the redox status and the relevance of the reactive N species, nitric oxide (NO), during the primary N response (PNR), a process that involves the NRT1.1 nitrate (NO_3^{-}) transceptor, CBLs and CIPKs as well as other elements, including the phosphorylation of the NLP7 transcription factor and the subsequent induction of NO_3^{-} responsive genes. The authors argued that NO plays a major role in the induction of the genes involved in redox regulation and NO_3^{-} assimilation, mediated by NLP7, and further discussed the possible ways by which NO exerts that action. On the other hand, Chen et al. (2024) extended the current paradigm of NO_3^{-} transport in pea (*Pisum sativum*). Following a genomic survey of NRT2 coding genes, one group of NRT transporters, they provided evidence - based on the use of over-expressing and RNAi lines - that in this crop legume the *PsNRT2.3* gene encodes a functional high-affinity NO_3^{-} transporter relevant for the transport of NO_3^{-} from low NO_3^{-} solutions, whose expression is stimulated by NO_3^{-}. Furthermore, the authors showed that PsNRT2.3 physically interacts with PsNAR, a NO_3^{-} assimilation-related protein, and that silencing of *PsNAR* reduces the NO_3^{-} uptake capability, thus indicating the widespread interaction between these proteins for the capture of this chemical form of N as already observed in other crops. Zhang et al. (2024) showed that, consistent with previous observations, exposure to

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low NO_3^- supply promotes the suberization of the root endodermis. The authors further explored the mechanisms involved in, and the consequences of, this process in tobacco plants. While the functionality of the apoplastic pathway of transport may be altered, as revealed by the use of the apoplastic tracer dye PTS, no obvious relationship was found between root suberization and NO_3^- uptake. The authors advanced evidence on the interplay between abscisic acid (ABA) and root suberization during plant response to N deficiency.

A major issue in contemporary agriculture is to minimize the input of N-based fertilizers and make the use of this functional element more efficient. This can be done by using multiple strategies as here exemplified by four works in tomato plants. Noticeably, tomato plants can reduce the need for NO_3^- supply through the use of chloride (Cl^-) as shown by Lucas et al. (2024). The authors informed that over a wide range of NO_3^- supply, the addition of Cl^- does not enhance the accumulation of NO_3^- within plants, while helping to reduce N deficiency symptoms, maintain the photosynthesis and increase the antioxidant capacity at low N levels. Furthermore, Cl^- positively impacts the water status of the leaves, particularly under moderate NO_3^- supply. These findings reinforce the possibility of using the beneficial element Cl^- as a tool to maximize N use efficiency. Colman et al. (2024) explored an alternative way to reduce the need for N provided as NO_3^-. In this regard, the authors offered evidence indicating that supplementation of the growing media with chitosan microparticles (CS-MPs) limits the detrimental effects exerted by suboptimal N levels on aerial biomass and chlorophyll content under long-term N deficiency. The authors further showed that the addition of CS-MPs impacts root NO-associated fluorescence, as well as the expression of genes involved in N capture and assimilation. These findings highlight the potential use of CS-MPs to alleviate N deficiency symptoms in plants growing under low-nitrogen soils. Showing the multiplicity of procedures to improve the performance of plants under conditions of limiting N supply in this issue Renau-Morata et al. (2024) studied the consequences of grafting between rootstocks of tomato plants overexpressing Cycling DOF Factor 3 genes from either *Arabidopsis* or tomato (*AtCDF3* and *SlCDF3*, respectively), and non-transformed scion, under different N inputs. The authors found that grafting with *AtCDF3*-expressing plants, but not with *SlCDF3*, results in increased biomass and fruit yield, in a way related to major physiological and biochemical changes, including a greater production of sugars and amino acids. The authors explored the role of hormones and disclosed the possibility that the differential mobility of the *AtCDF3* transcript through the phloem could explain the distinct effects exerted by the overexpressed genes. Complementary to biotechnological approaches, screening of populations for variation in N use efficiency (NUE) and related traits, may be a straightforward procedure. In this regard, Flores-Saavedra et al. (2024) examined a collection of thirty tomato accessions under high and low N supplies. They found that the growth performance was affected by both the genotype and the N availability. By dissecting the components of NUE into the uptake (NUpE) and utilization (NUtE) efficiencies, the authors found that NUpE positively correlates with root biomass at high N supply, while NUtE correlates with a high C/N ratio. The variability found among accessions suggests that some marker traits may be used for screening plant genetic resources under contrasting conditions of N supply. Interestingly one of the accessions examined performs well in both high and low N supply, thus advocating its suitability to be used in different environments.

3. Acclimation responses to low functional plant element supply

Although N supply can frequently limit crop production, other functional elements - including those required in small quantities - can affect productivity. As an example of this statement, it has been shown that low soil Fe availability could negatively affect crop yield while reducing the nutritional quality of the grains. Exploring the mechanisms determining genotypic differences in the tolerance to low Fe supply could help to limit Fe fertilizer practices and shed light on traits to be pursued in breeding programs. In this Issue, Meena et al. (2024) studied two wheat genotypes with contrasting tolerance to Fe deficiency and explored the mechanisms that could account for this difference. A transcriptome-based approach demonstrated that Fe uptake and mobilization pathways are overrepresented in the line tolerant to Fe deficiency as compared to the susceptible one, under conditions of metal scarcity. This result was reflected in a high Fe translocation index and phytosiderophore (PS) release from the roots. Based on the fact that Zinc-induced facilitator (ZIFL) coding genes were highly expressed in the wheat line tolerant to Fe deficiency and, utilizing TILLING (Targeting Induced Lesions in Genomes) technology and yeast complementation assays, TaZIFL4.2 was identified as a PS efflux transporter that could contribute to tolerance to Fe deficiency in wheat. Another element that frequently limits crop production is P. Mani et al. (2024) studied a group of phosphate transporters (PHO1) in the legume chickpea (*Cicer arietinum*). The authors identified five *CaPHO1* genes and characterized their expression patterns at different developmental tissues, nodules, and under P deprivation. By complementation studies using the Arabidopsis *pho1* mutant as well as by using chickpea RNAi knock-down lines, the authors showed that three CaPHO1 members (CaPHO1, CaPHO1; like, and CaPHO1; H1) have a crucial role in root to shoot P movement, and function redundantly to maintain inorganic P homeostasis and nodulation in chickpea. As previously mentioned, the acquisition and utilization of mineral elements depends on their availability in the soil which, in the context of climate change, may be severely affected by other stress conditions, including changes in precipitation regimen. In this context, Esfahani and Sonnewald (2024) discussed the interactive effects of water and P availability, two crucial factors for adequate plant growth. Given that P and water may show different distributions in the soil (topsoil and subsoil respectively), the ability to adjust root system architecture to cope with contrasting distributions is a challenge for breeding crop plants with enhanced tolerance to both stress conditions, low P and water scarcity, which require a deep knowledge of the root traits, the regulatory gene network involved, and the resulting effectiveness to explore the soil for nutrient and water. Ideotype models for "topsoil, subsoil, and topsoil/subsoil foraging" for monocot and dicot plants coupling root traits for water- and P-efficient cultivars were proposed.

4. Mineral elements and their toxic effects

Mineral elements found in native or polluted soils may, in some cases, negatively affect plant performance, particularly at high supply levels. One of the most abundant elements in the Earth's crust is aluminium (Al), which has been shown to play dual roles, being beneficial in some specific contexts while reports of Al toxicity are frequent for acidic soils. In this issue, Guo et al. (2024) presented an interesting review of the relationship between the regulation of stomatal movement and Al toxicity. As already mentioned, the latter is of particular interest in the context of soil acidification and anthropogenic contamination. Despite the existence of some gaps in the current knowledge about the role of Al in guard cell signaling, the authors have been able to present an updated revision on the plays and players, including ABA, reactive oxygen species (ROS), Ca^{2+}, and CO_2, involved in stomatal closure induction, while indicating potential strategies to improve Al tolerance by intervening with signaling processes. The global scenario also indicates the growing accumulation of other metals. As metal pollution affects plant growth and productivity, great efforts are currently devoted to deciphering the basis of plant metal tolerance. In this issue, Liu et al. (2023) identified 26 cadmium resistance (PCR) genes through a bioinformatic approach and characterized their expression profiling in *Brassica napus.* Focused on the *BnPCR10.1* gene, the authors explored its biological role using yeast functional complementation assays and heterologous expression in Arabidopsis. Their findings indicate that BnPCR10.1 is a copper (Cu) and cadmium (Cd) transporter localized in the plasma membrane, which could contribute to the tolerance to toxic levels of these metals by controlling the net root flux.

Even elements playing a major role in nourishing and signaling, and typically accumulated in large quantities, could also exert toxic effects depending on the ionic form prevalent in soils, such as occurs with N when provided in large quantities in the form of NH_4^+. In this issue, Marín-Peña et al. (2024) explored the role of root phosphoenolpyruvate carboxylase (PEPC) activity in the tolerance of sorghum (*Sorghum bicolor* L.) plants to NH_4^+ toxic levels. Plants growing under high NH_4^+ levels display induced N assimilation which, consequently, requires the continuous supply of carbon skeletons from the tricarboxylic acid cycle (TCA). The authors addressed the relevance of the non-photosynthetic PEPC and the TCA cycle for sorghum grown under high NH_4^+ nutrition as compared with NO_3^-, as sole N sources, by using RNAi lines that display decreased expression of the main PEPC isoform SbPPC3, thus exhibiting reduced root PEPC activity. These RNAi lines showed NH_4^+ hypersensitivity and altered TCA functioning. This work helps to connect the dynamics of carbon and N under this important mineral stress condition. On the other hand, Dziewit et al. (2024) explored if changes in the content of cytokinin are related to the NH_4^+ toxicity syndrome in Arabidopsis. A complete metabolic overview of cytokinin metabolism was analyzed in leaves and roots of plants cultivated on NO_3^- or NH_4^+ as the only nitrogen sources, including changes in cytokinin biosynthesis, conjugation and degradation. In addition, authors traced cytokinin levels in the root cap by confocal microscopy. Interestingly different metabolic mechanisms seem to set the active cytokinin pools in leaves and roots. Furthermore, the analysis of the whole root and apical root tips contributed to clarify a possible contribution of these growth regulators to shallow/short roots evidenced under solely NH_4^+-fed conditions.

5. Always silicon

Emanuel Epstein, thirty years ago (1994), attracted the attention of the scientific community to the fact that silicon (Si) is a frequent constituent of plant tissues although its role in the biology of plants remained uncertain. That pioneering work was the milestone of a full exploration of Si - which continues nowadays - unveiling the pivotal role of this element in multiple aspects of plant life. Seeking for the development of sustainable tools/practices to improve plant resilience to climate change, in this issue Rachappanavar et al. (2024) presented a comprehensive and updated review on the role of silicon in plant responses to both biotic and abiotic stress, highlighting its role in fruit crop production, and the potential use of silicon-based fertilizers to cope with multiple and frequently interacting forms of stress. A major issue tackled by these authors referred to the molecular devices implied in Si movement within plants, including a subgroup of aquaporins, the nodulin 26-like intrinsic proteins (NIPs). The work of Thakral et al. (2023) provided the results of a search of aquaporins in mungbean (*Vigna radiata* L.), identifying nineteen members of the NIP subfamily, and then examining the structure of the selectivity filter of some of them by using dynamic simulation. They further explored their possible role in the transport of metalloids. The authors found that, when heterologously expressed in the yeast system, VrNIP2-1 has the capacity to mediate the transport of arsenic (As) and germanium (Ge), which share some physicochemical properties with Silicon, which proved to be acquired through the activity of this transporter. The authors highlighted the potential for the use of Silicon in agriculture by enhancing its uptake while reducing that of other metalloids like As and Ge.

Taken together the contributions here compiled add valuable information on the way how plants sense and respond to the stress imposed by excess or deficit of different mineral elements. They also help to understand the mechanisms involved in determining the tolerance to nutritional and combined stresses as well as their impact on the efficiencies of acquisition and utilization of functional mineral elements.

Declaration of competing interest

The authors declare no financial or personal conflict of interest for the work reported in this paper.

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Andrea Galatro

Instituto de Fisiología Vegetal (INFIVE), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de La Plata (UNLP), Diagonal 113 N° 495, 1990, La Plata, Buenos Aires, Argentina

Fisicoquímica, Facultad de Farmacia y Bioquímica, Universidad de Buenos Aires (UBA), Junín 953, 1113, Ciudad Autónoma de Buenos Aires, Argentina

Susana Gallego

Instituto de Química y Fisicoquímica Biológicas, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Universidad de Buenos Aires (UBA), Junín 956, 1113, Ciudad Autónoma de Buenos Aires, Argentina

Carlos García-Mata

Instituto de Investigaciones Biológicas, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata (UNMdP), Déan Funes 3240, Mar del Plata, 7600, Argentina

Ramiro Lascano

Unidad Ejecutora de Doble Dependencia, Instituto Nacional de Tecnología Agropecuaria (INTA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Unidad de Estudios Agropecuarios, Av. 11 de septiembre 4755, CP. 5014, Ciudad de Córdoba, Argentina

Guillermo E. Santa-María*

Instituto Tecnológico Chascomús, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Escuela de Bio y Nanotecnologías, Universidad Nacional de San Martín, Avda. Intendente Marino km 8.2, Chascomús, 7130, Buenos Aires, Argentina

* Corresponding author. Instituto Tecnológico Chascomús, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Escuela de Bio y Nanotecnologías, Universidad Nacional de San Martín. Avda. Intendente Marino km 8.2, Chascomús, 7130, Buenos Aires, Argentina.

E-mail address: gsantama@intech.gov.ar (G.E. Santa-María).