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REVIEW

Approaches and determinants to sustainably improve crop production

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Abstract

Plant scientists and farmers are facing major challenges in providing food and nutritional security for a growing population, while preserving natural resources and biodiversity. Moreover, this should be done while adapting agriculture to climate change and by reducing its carbon footprint. To address these challenges, there is an urgent need to breed crops that are more resilient to suboptimal environments. Huge progress has recently been made in understanding the physiological, genetic and molecular bases of plant nutrition and environmental responses, paving the way towards a more sustainable agriculture. In this review, we present an overview of these progresses and strategies that could be developed

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to increase plant nutrient use efficiency and tolerance to abiotic stresses. As illustrated by many examples, they already led to promising achievements and crop improvements. Here, we focus on nitrogen and phosphate uptake and use efficiency and on adaptation to drought, salinity and heat stress. These examples first show the necessity of deepening our physiological and molecular understanding of plant environmental responses. In particular, more attention should be paid to investigate stress combinations and stress recovery and acclimation that have been largely neglected to date. It will be necessary to extend these approaches from model plants to crops, to unravel the relevant molecular targets of biotechnological or genetic strategies directly in these species. Similarly, sustained efforts should be done for further exploring the genetic resources available in these species, as well as in wild species adapted to unfavourable environments. Finally, technological developments will be required to breed crops that are more resilient and efficient. This especially relates to the development of multiscale phenotyping under field conditions and a wide range of environments, and use of modelling and big data management to handle the huge amount of information provided by the new molecular, genetic and phenotyping techniques.

KEYWORDS

climate change mitigation, drought, heat stress, nitrogen, phosphate, salinity

1 | INTRODUCTION

Future food and non-food crop production will require both increasing yield and reducing losses due to the environment in the context of a fluctuating climate. The increasing frequency of extreme weather conditions, such as heatwaves, drought and flooding, dramatically affects agricultural productivity negatively (FAO, 2021; Ray et al., 2015). In the last decades, agriculture largely relied on the use of pesticides, inorganic fertilizers and irrigation to combat stress. The steady rise in nitrogen (N) fertilizer consumption, as initiated after the Second World War, may still increase 2.5-fold by the year 2050 (Tilman et al., 2011). This massive use has expanded the pool of reactive N in the environment with significant environmental consequences (Swarbreck et al., 2019) due to the low recovery of N fertilizers by crop plants. In some cases, <40% of the applied N is taken up by the crop (Sylvester-Bradley & Kindred, 2009) and the remainder is lost within the agro-ecosystem. The environmental impact of N excess is multiple, including eutrophication of aquatic ecosystems, groundwater pollution, soil acidification, greenhouse gas emissions and consequent global warming, decrease in global species diversity and deleterious effects on human health. Phosphorus (P) is another essential plant micronutrient with a major impact on crop productivity. It remains unevenly distributed in soils across the world, and the use of phosphate (Pi) amendments is therefore necessary to sustain yield. The demand for P fertilizer steadily increases from 1.3 to 2% per year. However, the phosphate rock (the source of P fertilizer) is a finite natural resource and most of it contains high levels of toxic metals (Benredjem et al., 2016). Only a small part of P amendments (20%–25%) is recovered by plants as Pi has a very poor mobility in soils and Pi forms insoluble complexes with many soil cations or adsorbs to clays, resulting in reduced bioavailability for roots. The excess of Pi promoted leaching leads to algal bloom of cyanobacteria and subsequently to rivers and lake eutrophication. Besides excessive N and P fertilization, intensive irrigation is widely used to stabilize yield and counteract consequences of global warming. However, irrigation threatens water resources for human consumption and induces salinization of vast areas endangering food production. Moreover, droughts are increasing in their frequency and spreading in previously unaffected farming areas, such that irrigation is an increasingly unsustainable agronomic practice. Climatic events that constitute heat stress which reduce yield through multiple processes are also increasing in both their frequency and severity in key crop growing regions. Accordingly, there is an urgent need to breed for varieties that are more productive under a wide range of environments and more resilient to suboptimal growth conditions. In the frame of the H2020 CropBooster-P project, a research initiative that prepares a roadmap for the development of improved crops to future-proof European agriculture, we explored options to sustainably meet our future crop production. Here, we propose to review the recent progress made in the understanding of the physiological, genetic and molecular bases of plant nutrition and environmental responses in model plants and explore the opportunities for crop breeding through examples of how plants respond to fluctuating environment (water, salinity and heat stress) and nutrition state (N and P).

2 | WATER, SALINITY AND HEAT STRESS

2.1 | Improving water uptake and transport by roots

In view of global climate change and strong water demand from agriculture, water deficit is recognized as the abiotic stress that affects crop productivity the most (Peng et al., 2020). Europe already faces a declining water availability and higher variability in precipitation, both in space and time, translating into increased risks of water stress on crops and significantly impacting European agriculture. Drought not only alters plant productivity but also has a significant impact on plant quality, for example cell wall composition, affecting digestibility by cattle or microorganisms for biofuel production (Ezquer et al., 2020). While controlled water deficit may improve fruit quality through a higher concentration of flavour or antioxidant compounds, drought often decreases crop nutritional quality (Gasparini et al., 2021). Accordingly, a better understanding of plant responses to water availability is of utmost agronomic importance to improve crop productivity and quality.

Water is taken up by roots and transported through xylem vessels up to the leaves where it is evaporated through stomata. The different steps of water uptake, transport and water status sensing have been subjected to intensive research as targets for drought tolerance (Maurel & Nacry, 2020). One of the most promising targets to improve drought tolerance is root architecture and functions. Root system architecture (RSA) can be defined by length (depth) of the main root(s), the density and elongation of lower order roots, their gravitropic set-point angle and the possible presence of crown roots or adventitious roots. Selection of root traits is complex as roots vary with soil type and rainfall, and requires considerable investment for functional assays or growth monitoring in the field. However, studies performed in controlled and field conditions on land races and large panels of genotypes showed that a reduction in the number of shoot born roots (Gao & Lynch, 2016; Sebastian et al., 2016) and deep rooting is important parameters for water capture when deep water is available (Gao & Lynch, 2016; Kulkarni et al., 2017; Uga et al., 2011, 2013). Accordingly, modulating the expression of rice CROWN ROOTLESS 1 (CRL1) (Coudert et al., 2015) or DEEPER ROOTING 1 (DRO1) (Uga et al., 2013) can reshape the RSA to optimize water capture. Similarly, maize lines with fewer lateral roots (Zhang et al., 2016), reduced cortical cell layers (Chimungu et al., 2014a) or promoting aerenchyma formation (zhu et al., 2010) were found to be more resistant to drought possibly through increased carbon allocation to meristems promoting deeper rooting. These elements support the 'steep cheap and deep' (SCD) ideotype that was proposed to be optimal for water acquisition (Lynch, 2013). However, these ideotypes may not be optimal for quick recovery after drought in seasonal precipitation regimes or for acquisition of nutrients, such as phosphate which lay in patches in superficial soil layers. It was observed that *Arabidopsis thaliana* accessions with shallow rooting systems are more tolerant to drought (Ogura et al., 2019), suggesting that a more horizontally distributed root system might be an adaptation to efficiently capture water in environments with sparse rainfall. A proliferating root system was also proposed to extract more water and nutrients under stress conditions in maize (Ruta et al., 2010), legumes (Ye et al., 2018) and trees (Ramirez-Valiente et al., 2018). Similarly, maize roots with increased diameter (Chimungu et al., 2014b) or increased lignification of cortical sclerenchyma (Schneider et al., 2019) improved root depth and plant growth under mechanical impedance that is often associated with drought.

In addition to modulating growth, recent studies have shown that roots can sense moisture gradients and direct their growth or position lateral roots preferentially towards increased water availability. These local adaptations to water availability are referred to as hydrotropic response (Dietrich et al., 2017) and hydro-patterning (Orosa-Puente et al., 2018), respectively. Finally, Rosales et al. (2019) showed that roots have a differential adaptive response to water availability depending on their age and rank. Engineering and fine-tuning the expression of genes controlling cell division and elongation open avenues for breeding more extensive and efficient root systems.

Water uptake is also critically determined by the intrinsic water transport capacity of roots, referred to as root hydraulics. Whereas aquaporins, water channel proteins that facilitate water diffusion across cell membranes, have been well characterized (Maurel et al., 2015) and identified as targets to improve drought tolerance (Ding et al., 2020; Shekoofa & Sinclair, 2018), many other components of root hydraulics remain to be discovered. For instance, the crucial role of deposition of lignified and suberized barriers in the exodermal and endodermal cell wall layers and controlled by specific MYB and NAC transcription factor (TF) clades remains largely underexplored (Barberon et al., 2016). Similarly, quantitative genetic approaches in the model plant Arabidopsis identified HYDRAULIC CONDUCTIVITY OF ROOT 1 (HCR1), a Raf-like MAP3K protein kinase (Shahzad et al., 2016) or XYLEM NAC DOMAIN 1 (XND1), a NAC DOMAIN TF (Tang et al., 2018) as important regulators of root hydraulics, with crucial and specific roles under water excess and deficit, respectively. These examples illustrate the power of natural variation approaches for identifying new and unexpected regulators to dissect and possibly improve root hydraulic performance under agricultural conditions.

2.2 | Regulation of water losses

When subjected to water limitation, plants primarily maintain their water status by regulating transpiration through stomatal opening and closing. Stomata serve dual and often conflicting roles, facilitating carbon dioxide influx into the leaf internal tissues for photosynthesis and regulating water efflux via transpiration. Accordingly, stomata have been the centre of interest for improving drought tolerance (reviewed by Lawson & Blatt, 2014). Many studies exploiting natural genetic variation or overexpressing genes such as the *ERECTA* or *EPIDERMAL PATTERNING FACTOR 1* (*EPF1*) have shown that reduction of stomatal density in *Arabidopsis*, rice (*Oryza sativa*), wheat (*Triticum spec.*) or tobacco (*Nicotiana tabacum*) significantly enhances drought tolerance by reducing water losses, with very limited reduction of growth under optimal conditions (Caine et al., 2019; Kulkarni et al., 2017; Liu et al., 2019; Yu et al., 2013). The regulation of stomatal opening is of particular interest to limit water losses. Several signalling pathways involving reactive oxygen species (ROS) production (Hu et al., 2017) or chloroplast retrograde nucleotide phosphatase signalling (Zhao et al., 2019) have successfully been targeted. The most studied and engineered pathway relies on the phytohormone abscisic acid (ABA). ABA mediates rapid stomatal closure to maintain the leaf water status when the evaporative demand becomes too high. Accordingly, the manipulation of ABA production or sensitivity significantly promotes drought tolerance in many species including model species, crops or woody plants (Guo et al., 2019; He et al., 2018; Lawson & Blatt, 2014; Pedrosa et al., 2017; Yang et al., 2016, 2019). However, ABA does not only control stomatal opening but also long-term growth and metabolic adjustments allowing plants to tolerate extended periods of water deficit (Cutler et al., 2010; Zhao et al., 2016). ABA also regulates root and shoot development, metabolism, nutrient sensing, growth or plant-pathogen interactions (reviewed by Yoshida et al., 2019). The molecular and cellular processes underlying these responses and their integration at the whole plant level remain poorly understood. Nonetheless, recent progresses in deciphering the complex regulatory networks of ABA perception and signalling in Arabidopsis, including ABA receptors, kinases, TF and stabilizing PP2C protein complexes (Zhao et al., 2016), bring new perspectives to improve drought tolerance in crops. In Arabidopsis, targeted modification of the PYRABACTIN RESISTANCE (PYR/PYL) ABA receptors led to an increased growth rate under water deficit conditions and an increase in water use efficiency (WUE) by 40% (Yang et al., 2016, 2019). Similar results were also obtained in rice where combinatorial targeted mutations in PYR 1;4 and 6 ABA receptors controlled stomatal opening under drought with reduced detrimental effects on seed dormancy and plant growth (Miao et al., 2018). Similarly, new agonists of ABA receptors which can locally and specifically trigger signalling pathways are shown to improve plant tolerance to water stress by closing stomata with very limited side effects on plant growth (Mosquna et al., 2011; Okamoto et al., 2018). Similarly, an in-depth understanding of the functioning and regulation of the guard cells surrounding the stomatal pores identified ion fluxes as key regulators of stomatal opening. For instance, the expression of an engineered BLUE LIGHT-INDUCED K^+ 1 (BLINK1) channel in Arabidopsis guard cells accelerated both stomatal opening and closure and significantly increased biomass production in fluctuating light conditions without any cost in plant water use (Papanatsiou et al., 2019). Similar strategies could be considered to force stomatal closure at night, thereby limiting water losses without altering growth (Coupel-Ledru et al., 2016). These examples illustrate the potential of targeted manipulation of ABA signalling pathways or stomatal kinetics to improve WUE without penalty in carbon fixation, paving the way for future engineering approaches.

2.3 | Optimizing water deficit sensing, phenology and development to improve drought tolerance

Studies investigating the early perception of water deficit by roots identified candidate genes such as REDUCED HYPEROSMOLALITY, INDUCED CA2+ INCREASE 1 (*OSCA1*) and key downstream messengers, such as ROS and calcium (Hamilton et al., 2015; Martiniere et al., 2019; Yuan et al., 2014). Yet, most of the molecular and cellular mechanisms involved remain largely unknown. Roots can adapt to heterogeneous water resources or rapid changes in salinity in the soil or to fluctuating water demands from the shoots (see hereafter). This capacity indicates that roots must continuously emit or sense systemic signals transferred within the root system or between roots and shoots (McLean et al., 2011; Puertolas et al., 2015). To date, only a single dehydration-induced peptide that relays root signalling towards shoots has been uncovered (Takahashi et al., 2018), but other physical (such as hydraulic), chemical (hormones, ions and ROS) or molecular (mRNAs or ncRNAs) signals are likely to be involved in the root responses to heterogeneous or varying water availabilities.

Other traits such as shoot architecture are promising targets. For instance, more erect leaves can significantly reduce the transpiration rate (Van Zanten et al., 2010) and the meristem temperature, preventing an earlier cessation of development (Jagadish et al., 2021). Another direction is to breed for phenological traits, such as earliness, to reduce the risk of being exposed to water deficiency periods in wheat (Kulkarni et al., 2017; Le Gouis et al., 2012), maize (Parent et al., 2018) or woody plants (Allard et al., 2016). Delayed leaf senescence has also been shown to enhance tolerance to drought, to increase grain yield and biomass production and to improve horticultural performances of many species (Guo & Gan, 2014). In contrast to annual crops, forest trees or grapevine is long-lived organisms that are subjected to repeated environmental constraints throughout their lifetimes. Accordingly, they are facing specific threats such as drought-induced xylem blockages (e.g. embolisms) resulting in a decline in sap flow observed under severe and/or repeated water deficits (Maurel et al., 2015). Understanding and manipulating xylem properties is therefore also of major interest for stress adaptation and plant survival (Brodersen et al., 2019).

2.4 | Harnessing the genetic diversity of plants for drought tolerance

Besides these hypotheses-driven approaches, several research programmes have recently pointed epigenetic regulations as a powerful and possibly conserved process for plant acclimation to fluctuating and harshening environments (Sow et al., 2018). For instance, Ma et al. (2019) identified in rice a chromatin regulatory process via histone ubiquitination/de-ubiquitination that modulates its capacity to cope with drought stress. Characterizing the underlying mechanisms in other annual and perennial species will identify new breeding targets to improve acclimation to repeated periods of water deficit. In addition to epigenetic modifications, a large number of breeding programmes based on biomass production, yield or nutritional quality under water deficit have identified thousands of yet uncharacterized quantitative trait loci (QTLs) in many crops including cereals (Budak et al., 2015; Li et al., 2016; Ruta et al., 2010; Tuberosa & Salvi, 2006) legumes (Ye et al., 2018), oleaginous crops (Masalia et al., 2018), fruits (Albert et al., 2016), forage and biomass producers (Shinozuka et al., 2012; Van der Weijde et al., 2017) and woody plants (Allard et al., 2016; Tandonnet et al., 2018). Though difficult to handle, marker-assisted selection allowed breeders to manipulate and combine these QTLs to improve drought-related traits. However, the genetic bases of the molecular, cellular and developmental responses underlying these QTLs remain mostly uncharacterized. Developments in genomic-based approaches will provide access to agronomically desirable alleles present in these QTLs. In the future, combination of high-throughput sequencing and deep learning analyses will facilitate the identification, cloning and engineering of genes at target QTLs, representing an extraordinary resource for improving drought tolerance. However, harnessing the full potential of these technologies will initially require an integrated knowledge of the molecular phenotypic and the physiological processes underlying water deficit tolerance.

2.5 | Engineering plant salt stress tolerance

Soil salinization is related to the long-term and continuous discharge of saline groundwater (primary salinity), or to human activities (secondary salinity) such as irrigation with saline groundwater. Also, dryland salinity is related to rising groundwater tables bringing salt with it in surface soil, in non-irrigated areas. As the soil surface dries out, salt is left in surface soil. These phenomena cause an increase in salt concentrations in the root zone, particularly under high evaporation and low leaching by rainfall or irrigation with freshwater which represents the main management to ameliorate salt-affected soils. Also, coastal agriculture is threatened by salinity problems due (1) to pumping of freshwater in the coastal aquifers which provokes saltwater intrusion and (2) to sea level rise, ingress of sea water through wind transport of salt spray or storms. FAO estimated that ~20% of irrigated lands worldwide are salt-affected. Each year, about 10 million ha of agricultural lands are destroyed by soil salinization (Pimentel et al., 2004). Saline soils affect plant growth and development due to the excess of soluble sodium ions (Na^+). Plant species exhibit a distinct degree of tolerance to salt stress. In cereals for instance, the most tolerant species are barley (*Hordeum vulgare*), bread wheat (*Triticum aestivum*) and durum wheat (*Triticum turgidum ssp. durum*), whereas rice is the most sensitive species (Munns & Tester, 2008).

A two-phase model has been proposed, with an early plant response corresponding to an increase in external osmotic pressure, similar to what occurs upon water stress, and a slower response due to accumulation of Na^+ in the shoot (Munns & Tester, 2008). Visual symptoms of salt injury are leaf tip burns, leaf browning and death, reduced plant growth, poor root growth, sterility and reduced seed production. Salt stress also impairs photosynthesis both by reducing stomatal conductivity and transpiration (Fricke et al., 2004) and by the specific toxicity of Na^+. Indeed, Na^+ competes with K^+ at binding sites in key metabolic processes such as enzymatic reactions and protein synthesis, albeit that Na^+ cannot entirely replace K^+ as a coordinating ion (Nieves-Cordones et al., 2016). Excess of Na^+ which competes with K^+ transport also impairs polarization of plant cell membrane potential, which is crucial for the entry and exit of solutes (Nieves-Cordones et al., 2016; Shabala, 2009). As salt stress induces rapid and massive oxidative stress, it was suggested to develop engineered lines overexpressing antioxidant molecules, such as polyphenols, flavonoids or ascorbate (AbdElgawad et al., 2016). Engineering compatible solute accumulation such as sucrose, proline or glycine betaine to counteract salt-induced osmotic stress has been extensively performed in crops with some success (Lutts et al., 1996; Mattioni et al., 1997; Misra & Saxena, 2009). However, validation of this strategy was performed in very restricted conditions, or limited developmental stages rendered this approach marginal (Shabala, 2009). Since salt stress induces a reduction in root hydraulic conductivity in several crop species, such as barley (Horie et al., 2011), manipulation of aquaporin expression, such as *OsPIP1;1* in rice, has been attempted but did not lead to conclusive results (Liu et al., 2013).

A strategy to exclude Na^+ from root cells relies on the extrusion of this toxic ion from root epidermal cells. Indeed, Na^+/H^+ antiporter SALT OVERLY SENSITIVE 1 (SOS1) is a critical salt tolerance determinant in plants, by playing this role of Na+ exclusion. In rice, OsSOS1 maintains a low concentration of this toxic ion in the cytosol (Martinez-Atienza et al., 2007). Tolerance of tissue to accumulated Na^+ is related to compartmentalization of Na^+ at the intracellular level to avoid toxic concentrations within the cytoplasm, especially in mesophyll cells in the leaf. Hence, Na^+ is compartmentalized into vacuole by Na^+/H^+ antiporter type SODIUM/HYDROGEN EXCHANGER 1 (NHX1) (Fukuda et al., 2004). Similarly, preferential expression of Na^+-selective influx transporter of the HYDROGEN/POTASSIUM TRANSPORTER 1 (HKT1) family in root xylem parenchyma and in cells adjacent to phloem vessels in leaves leads to the unloading of Na^+ from the root xylem (Venkataraman et al., 2021). This leads to the retention of this ion in root cells preventing its accumulation in shoot (Chen, Hu, et al., 2015; Chen, Wang, et al., 2015; Ren et al., 2005) OsHKT1 is located at the Saltol QTL identified for salt tolerance (Chen, Hu, et al., 2015; Chen, Wang, et al., 2015). RSA might also be an important parameter to be controlled for salt tolerance strategy, since Na^+ was suggested to enter through lateral root emerging sites and root tip regions where the Casparian strips and suberin lamellae are disrupted or immature, respectively (Krishnamurthy et al., 2011). Hence, reducing lateral root density in the surface soil horizons and promoting earlier differentiation of secondary cell wall components are promising breeding targets specially in dry land areas. On the contrary, reduction of root deepness and increase superficial root system by modification of root cone angle via an allele of qSOR1, a DRO homolog, increases yield in coastal areas where sea level elevation threatens crop production (Kitomi et al., 2020). In the future, further knowledge may also result from the exploration of tolerance mechanisms in halophytes, glycophytes and wild relatives. In these species, mechanisms involving anatomical adaptations such as reinforced root apoplastic barriers (lignin and suberin deposition) or leaf salt glands likely act in addition to mechanisms detailed above.

2.6 | Improving heat stress tolerance

Climate change results in increased temperatures that are often negatively correlated with productivity and yield (Jagadish, Kavi Kishor, et al., 2015; Jagadish, Murty, et al., 2015; Ray et al., 2015). In addition, it leads to more frequent and severe heatwaves (Hao et al., 2013) which affect any crop species. Heat stress is defined by temperatures at which optimal plant functioning and homeostasis are impaired, leading to reduced growth, yield, quality and productivity (Ortiz-Bobea et al., 2019). Temperatures which impose stress are therefore dependent on the optimal values for a given species and variety. The significance of any given heat stress event is defined by the developmental stage it co-occurs with. Therefore, heat tolerance strategies can be developmentally distinct. For example, the capacity to maintain functional leaf chlorophyll can facilitate heat tolerance during vegetative growth, but this 'stay-green' capacity can be detrimental post-anthesis as it may limit senescence that is important for remobilizing stored carbon and nitrogen to yield (Jagadish, Kavi Kishor, et al., 2015; Jagadish, Murty, et al., 2015). The diel nature of heat stress events is also important for determining their severity. For example, dryland cereals, for example wheat, tend to initiate anther dehiscence in the early morning; therefore, early morning heatwaves can perturb fertility and yield, since pollen is very heat sensitive (Aiqing et al., 2018). Conversely, it is now established that high night-time temperatures, which increase disproportionately to daytime temperatures, can be hugely restrictive to yield especially during grain-filling periods and minimum temperatures correlate well with yield losses. Reductions in yield for cereals have been reported as between 1% and 9% for every 1°C increase in nocturnal temperature (for review see Schaarschmidt et al., 2021). Although there is still a lot to be understood about nocturnal heat stress, recent work shows clearly that enhanced respiration can divert photosynthates away from reproductive sinks and towards maintenance respiration. For example, high night-time temperatures have been demonstrated to increase flag leaf respiration rates, which was linked to a reduction in non-structural carbohydrates and reduced spikelets per panicle (Xu et al., 2021).

A clear mechanism by which yield is reduced is via the impairment of carbon fixation during photosynthesis, the alteration of the physiological processes within reproductive organs leading to sterility or if elevated temperatures persist during the grain-filling period, they can induce grain senescence, reducing grain weight and quality even further. This clearly indicates that the developmental stage is crucial when assessing the impact of heat stress on crop productivity. Regarding photosynthesis, electron transport systems and CO_2 reduction pathways are hugely sensitive to high temperatures (Ferguson et al., 2021; Moore et al., 2021). In particular, the RuBisCo carboxylase activity is curtailed by an enhancement of the oxygenase reaction leading to increased flux through the photorespiratory pathway (Crafts-Brandner & Salvucci, 2000; Perdomo et al., 2017) which further reduces the CO_2 assimilation capacity (Walker et al., 2016). Recent studies demonstrated the success of changing the rate of photorespiration to enhance yield (South et al., 2019). Accordingly, improving the thermal tolerance of the RuBisCo activase enzyme has been exploited to improve photosynthesis at higher temperatures (Perdomo et al., 2017) and ultimately enhance yield (South et al., 2019). As temperatures rise, rates of cellular respiration rise, consuming storage carbohydrates more rapidly. This induces unstable cellular conditions, disruption of both metabolism and membrane transport leading to an increase in oxidative stress and photoinhibition (Choudhury et al., 2017). In wheat, high temperatures induce lipid desaturation and oxidation, thereby damaging organelles and reducing the photosynthetic rate (Djanaguiraman et al., 2018). Protein stability is also altered at high temperature and wheat genotypes accumulating heat-shock proteins were shown to be more tolerant to heat stress damages. Similarly, heat-tolerant wheat lines were selected on increased chlorophyll fluorescence leading to improved photosynthetic efficiency (Ferguson et al., 2020; Sharma et al., 2015).

Crops display plastic developmental responses to temperature with progression through developmental stages of life cycles hastened substantially across species (Hatfield et al., 2011). Although high temperatures alter leaf morphology impacting light interception and CO_2 fixation via photosynthesis (Gray & Brady, 2016), reproductive development appears to be the most sensitive. Heat stress alters pollen viability (Zinn et al., 2010), induces asynchrony between male and female reproductive development (Hedhly et al., 2008; Herrero, 2003) and reduces the size and number of both carpels and stamens and pollen dispersal (Gray & Brady, 2016; Sato et al., 2002). In addition to altering plant fertility, high temperatures can also reduce grain quality in terms of protein content. Indeed, the expression of genes involved in the signalling pathways that elicit floral transitioning, flower development and grain filling are often dependent on temperature cues to adjust flowering time to the prevailing environmental conditions and maximize fitness. Consequently, elevated temperatures accelerate flowering time and reduce grain-filling periods and then will negatively impact yield (Ferguson et al., 2021; Hatfield et al., 2011). Elevated temperatures during the grain-filling period can also induce grain senescence, which in turn will reduce grain weight and quality even further. Heat tolerance is linked to N nutrition mainly through the timing of both carbohydrate and N storage in stems for grain filling. In wheat, for instance, heat stress accelerates carbohydrates remobilization, while it impairs the remobilization of nitrogen (Tahir & Nakata, 2005). Besides the above-ground parts of the plant, the below-ground parts exhibit important developmental responses to heat stress (Pinto & Reynolds, 2015). The development of an efficient root system for water extraction even under suboptimal conditions can maintain sufficient water supply to the canopy and then reduce its temperature via enhanced transpiration. Accordingly, QTLs for cool canopies were often associated with proliferation for rooting at depth under drought, or near the surface during hot and irrigated conditions in wheat (Pinto & Reynolds, 2015). Although studies involving other stresses, such as drought, have realized the importance of post-stress recovery, only very few studies have integrated tolerance and recovery (Janni et al., 2020). Examples of differential rates of recovery and the existence of physiological, molecular and genetic diversity in plants recovering from drought stress provide compelling evidence for developing heat stress-resilient plants (Jagadish et al., 2021).

It is worth noting that periods of drought and increased temperature events increasingly co-occur in major crop producing regions. Reduced water availability can have important consequences for heat tolerance strategies. While both stresses are well demonstrated to reduce photosynthetic efficiency, a key distinction is the response of stomatal conductance. Where water is available, stomatal conductance typically increases during heat stress to facilitate evaporative cooling via transpiration and maintain thermal safety margins. Stomatal closure has the potential to minimize cooling and impose greater thermal risk. The response of stomatal conductance and photosynthesis to combined heat and drought stress is critically understudied. However, emerging evidence suggests that plants that typically demonstrate isohydric behaviour characterized by low stomatal conductance may have an enhanced capacity to increase stomatal conductance during heat stress beyond leaf turgor loss in order to avoid critical leaf temperature points (Hussain et al., 2019; Marchin et al., 2021).

Breeding for more heat-tolerant crops therefore requires (1) to take into account the type of heat stress that may vary in terms of duration and intensity, that is heat shocks, heatwaves and long-term stress; (2) to consider the plant developmental stages; and (3) to integrate both heat tolerance and rapid recovery. The increasing utilization of phenomic approaches has enabled the demonstration of significant, heritable variation within key crop species for traits that underpin these dynamics (Ferguson et al., 2020; Sharma et al., 2017; Wen et al., 2017; Xu et al., 2017; Xu et al., 2021), highlighting the feasibility of breeding for heat tolerance.

3 | APPROACHES TO IMPROVE NITROGEN USE EFFICIENCY

3.1 | Improving nitrogen uptake and transport

Plants require nitrogen (N) in bigger quantities than any of the other mineral elements. Hence, yield increases after the Second World War—the so called 'Green Revolution'—were enabled by the massive use of N fertilizers produced from atmospheric N_2 by the energy-intensive Haber–Bosch process. The global rise in N fertilizer consumption and its low recovery by crop plants has a strong environmental impact (Swarbreck et al., 2019). However, as limited N availability is strongly threatening yield, the global use of fertilizers is projected to continuously increase (Tilman et al., 2011). Therefore, there is urgent need to investigate alternative strategies to markedly improve crop nitrogen use efficiency (NUE), in particular their nitrogen uptake efficiency (NUpE). These strategies may rely on modified agricultural practices with more sustainable agro-ecological approaches that call for a better use of the root microbiota for optimized N supply, including N_2 fixing symbiosis. Other complementary options would be to modify the goals of crop breeding, or to set up biotechnological strategies, to favour productivity at reduced fertilizer input and/or increased NUpE at high N supply. These strategies rely on the relevant use of previously characterized key genes governing the various steps of plant N nutrition. Over the last decades, this research field has progressed tremendously fast, and almost all important genes encoding transporters or enzymes involved in N acquisition and assimilation have been identified (Vidal et al., 2020). As these genes are present in all plant species investigated to date, their genetic manipulation was an early general strategy to improve NUE (Nacry et al., 2013; Vidal et al., 2020).

With the general exception of legumes, plants acquire N from two main inorganic sources in the soil solution, nitrate (NO_3^-) and ammonium (NH_4^+). It has often been proposed that NH_4^+ nutrition may be more favourable than NO_3^- nutrition, because it avoids the extremely high energy cost associated with the reduction of NO_3^- to NH_4^+ (Raven, 1985; Salsac et al., 1987). However, this theoretical advantage may be overestimated because NH_4^+ nutrition is associated with hidden energetic costs due to futile NH_4^+ cycling between root cells and the external medium (Britto & Kronzucker, 2002). Furthermore, even if the biochemical processes of NH_4^+ assimilation are more energy-saving than those of NO_3^- assimilation, they can contribute to the general toxicity syndrome affecting many plant species fed with NH_4^+ as predominant or sole N source (Britto & Kronzucker, 2002; Hachiya et al., 2021). Therefore, for most higher plant species, NO_3^- is the preferred N source and many attempts to enhance NUpE by overexpressing the low or high-affinity NO_3^- uptake transporter genes that belong to the NRT1 and NRT2 families respectively have been made. However, these resulted in only little success to date. A surprising exception is rice, which provided promising examples of transgenic approaches. For instance, localized overexpression of the high-affinity NO_3^- transporter gene *OsNRT2.1* with the *OsNAR2.1* promoter significantly increased NUE (Chen et al., 2016). Similarly, overexpressing *OsNRT2.3b*, an isoform of a further high-affinity transporter, increased not only NO_3^- but also ammonium uptake and improved grain yield and NUE by ~40% (Fan et al., 2016). Interestingly, plants overexpressing this short isoform of *OsNRT2.3* harbouring a truncated pH domain increased total N, P, iron (Fe) uptake and C metabolism by influencing pH homeostasis (Fan et al., 2016). The reasons why rice is such an exception compared to other species are not clear and may be related to the fact that lowland rice is mainly using ammonium as a N source, and thus, NO_3^- uptake has not been a breeding target.

3.2 | Improving nitrogen assimilation

Boosting N assimilation by overexpressing genes encoding nitrate reductase, the first enzyme of the NO_3^- assimilation pathway, has also been investigated. Although this sometimes led to more efficient NO_3^- assimilation in shoots, NUpE was not improved as root NO_3^- uptake was lowered (Gojon et al., 1998). This could be explained by a systemic feedback regulation, which down-regulates root NO_3^- transporter genes in response to a high organic N status of the plant (Nacry et al., 2013). The overexpression of a chloroplastic or cytosolic isoform of glutamine synthetase, a key enzyme in assimilating ammonia in organic compounds, led to an increase in grain yield in wheat (Hu et al., 2018) and an increased NUE in barley (Gao et al., 2019). Encouraging results were also reported with other enzymes of N-metabolism, such as alanine amino transferases (see Xu et al., 2012 for review). However, despite the positive effects achieved so far, it remains uncertain whether the simple manipulation of individual structural genes of N nutrition is a really promising approach to increase NUE.

Recent advances in deciphering the regulatory mechanisms of N uptake and metabolism may explain the limited progress in improving NUE by overexpressing individual target genes. First, the choice of the promoter driving the expression might be of tremendous importance, as strong ectopic overexpression may disturb key spatial or temporal aspects of N utilization. Second, root NO_3^- transporters or N assimilating enzymes are subject to strong post-transcriptional regulatory mechanisms (Jacquot et al., 2017), which may compensate for the effect of enhanced transcription. Third, it might be necessary to tune an entire pathway or even the interaction of several pathways such as the strongly interconnected N and C assimilation pathways to increase NUE and yield. Therefore, a more promising strategy may be to fine-tune the upstream genes of regulatory networks by engineering either key receptors, transcription factors (TFs) or other regulatory players. For example, the overexpression of the Dof1 TF, that is involved in N assimilation and C/N balance, resulted in an increased yield under low-N conditions in Arabidopsis (Yanagisawa et al., 2004) and in an increased yield in wheat (Peña et al., 2017). Similar results were obtained by overexpressing the TF *AtNLP7* that improved plant growth by enhancing N and C assimilation in Arabidopsis and tobacco (Yu et al., 2016), and by overexpressing *OsNLP4* in rice leading to an increased NUE and yield under moderate N supply (Wu et al., 2020). Similarly, overexpression of the TF *TaNFYA-B1* increased grain yield at low-N supply in wheat by enhancing both the expression of root NO_3^- transporters and the growth of lateral roots (Qu et al., 2015). Finally, other targets will also be the sensors of NO_3^- availability might be targets for improving NUE. Those identified to date surprisingly turned out to be also membrane transporters involved in root NO_3^- uptake. They are described as 'transceptors', due to their dual transporter/receptor function (Gojon et al., 2011). The Arabidopsis NRT1.1 (CHL1/NPF6.3) protein is the best described one and was shown to activate multiple signalling pathways governing a wide range of responses to NO_3^- (Bouguyon et al., 2015). In line with this hypothesis, overexpression of *OsNRT1.1B* (*OsNPF6.5*), the rice orthologue of *AtNRT1.1*, increased grain yield and NUE (Hu et al., 2015). Together, these data strongly suggest that strategies aiming at improving NUE should target upstream components of the signalling pathways such as those involved in the NRT1.1-dependent NO_3^- signalling for instance (Maghiaoui et al., 2020).

3.3 | Understanding and manipulating the N signalling pathways

Besides NO_3^- sensing, root NO_3^- uptake is also tightly controlled by the N status of the whole plant. This requires specific systemic signalling that relies on the long distance transport of signal molecules. Recently, (poly)peptides have been identified as key players (Ota et al., 2020). Three members of the glutaredoxin family of polypeptides (named CEPD1/2 and CEPDL2) were found synthesized in the shoot in response to N starvation. Subsequently, they are transported via the phloem down to the roots where they up-regulate root NO_3^- uptake through an increased expression of the major nitrate transporter gene *NRT2.1* (Ota et al., 2020). Although a lot remains to be discovered to fully understand the N signalling pathways, their elucidation is proceeding at an unprecedented pace. Indeed, during the last couple of years, hundreds of TF and associated target genes have been proposed to participate in the highly complex network of regulatory modules controlling N acquisition and assimilation (see Vidal et al., 2020). This provides a large list of candidate genes for further and more refined biotechnological or breeding strategies.

In the coming years, it will also be crucial to explore and exploit genetic resources to increase NUE as most breeding strategies developed to date have favoured yield, and not NUE, as the main criterion (Hawkesford, 2014). Accordingly, beneficial alleles for NUE might have been lost by recent selection, especially in cereals where the introduction of semi-dwarf mutations arising from the Green Revolution for their lodging resistance is known to be associated with a lowered NUE, due to imbalanced GRF4-DELLA interactions (Li et al., 2018). Reconsidering wild and ancestral germplasms will then be an important strategy in this matter. Several recent examples in rice demonstrate the potential of using ancestral germplasms. By a QTL study between a semi-dwarf and a natural rice variant, Li et al. (2018) identified the TF GRF4 as a new positive transcriptional regulator of multiple N-metabolism genes, which counteracts the negative effect of the DELLA growth repressors that accumulate in semi-dwarf lines. Using a genome wide association study (GWAS) in rice, Wang et al. (2018) have shown the grain number, plant height and heading date 7 (GHD7) TF as a causal locus for N accumulation. OsGHD7 acts upstream of ABC1 REPRESSOR 1 (ARE1), a protein with unknown function (Wang et al., 2021). Remarkably, the combination of the *GHD7* and *ARE1* alleles substantially improves NUE and yield performance under N-limiting conditions (Wang et al., 2021). Similarly, the tillering response to N supply that is closely correlated with NUE was studied in rice using a panel of rice germplasm collected from different eco-geographical regions (Liu et al., 2021). This GWAS approach identified TEOSINTE BRANCHED 1/CYCLOIDEA CYCLOIDEA/PROLIFERATING CELL FACTOR 19 (*OsTCP19*) as modulators of the tillering response to N supply. *OsTCP19* is at least partly regulated at the transcriptional level in response to N availability by Lateral Organ Boundaries Domain (*LBD*) TF, previously identified in Arabidopsis as regulators of N responses (Mukhopadhyay & Tyagi, 2015). Indeed, a 29-bp indel in the *OsTCP19* promoter can affect the repression effect of LBD proteins to *OsTCP19* expression (Mukhopadhyay & Tyagi, 2015). OsTCP19 regulates the expression of the tiller-promoting gene *DWARF AND LOW-TILLERING* (*DLT*), a component in brassinosteroid signalling, as well as the expression of genes involved in N assimilation (Mukhopadhyay & Tyagi, 2015). Moreover, choosing a population consisting of rice landraces with extreme N-related phenotypes, another GWAS identified a rare variant of a NITRATE TRANSPORTER 1/PEPTIDE TRANSPORTER FAMILY (*NPF*) family member, OsNPF6.1HapB, that improves NUE (Tang et al., 2019). Notably, the OsNPF6.1HapB allele has been lost in 90.3% of the rice varieties, probably due to the increased usage of N fertilizer. These several examples illustrate the power and great potential of genetic resources that have not been selected by breeding and must be explored in more of our crop species.

Although it has long been recognized that RSA is a key factor governing NUpE (Nacry et al., 2013), there is so far little progress on the definition and validation of root ideotypes. This is partly related to the methodological challenge of phenotyping root systems of adult plants in the field, but also to the strong plasticity of the root system in response to N availability, which is far from being fully understood. On the one hand, it is important to determine whether feasible phenotyping approaches are relevant for screening genotypes differing in NUpE in the field (Louvieaux et al., 2020). On the other hand, it is also crucial to strengthen the investigation of the signalling pathways shaping the RSA as a function of the N supply and/or demand. The number of candidate genes validated as key players in the N regulation of RSA is only a small fraction of the putative regulators identified in the N signalling pathways (Vidal et al., 2020). However, significant progress has been made, especially when considering the links between the N-induced responses of the RSA and the various hormonal signalling pathways. In Arabidopsis, N regulation of root growth and development was shown to involve many genes participating in auxin, cytokinins, abscisic acid or brassinosteroid synthesis, transport or signalling (reviewed in Jia & von Wirén, 2020). For instance, these include the NRT1.1 transceptor gene, the AFB3 auxin receptor gene, the TAR2 auxin biosynthesis gene, the ABI2 abscisic acid co-receptor gene, the ABCG14 cytokinin transporter gene and the BSK3 brassinosteroid signalling kinase gene. In addition, several transcription factors such as ANR1 and TCP20, and signalling peptides such as CLE and CEP peptides, play a significant role in modulating primary or lateral root elongation (Jia & von Wirén, 2020). Interestingly, homologues of the regulators listed above appear to play a similar role in other species than Arabidopsis, as shown for ANR1-like genes in rice (Yuan et al., 2014) or CEP peptides in Medicago (Chapman et al., 2020).

4 | APPROACHES TO IMPROVE PHOSPHATE USE EFFICIENCY

4.1 | Improving Phosphate uptake and transport

Improving phosphate (Pi) uptake and use is becoming a major concern due to the exhaustion of the natural P-rich rock resource and the strict regulations limiting the concentration of toxic metals in P fertilizers. Therefore, there is a need to distinguish between Pi uptake efficiency, for example traits that lead to greater acquisition of Pi from soil, from phosphate use efficiency (PUE). Indeed, PUE encompasses Pi acquisition, but also improving its overall utilization to increase production of the harvestable products (typically seeds). Accordingly, PUE includes the following: (1) improved soil exploration by roots, (2) Pi recovery in soils, (3) Pi uptake, (4) physiological use of Pi for growth and (5) yield production. Identifying the genetic basis of PUE traits has been performed in many species, and major QTLs have been mapped in rice (Wissuwa et al., 1998), maize (Chen et al., 2009), wheat (Yuan et al., 2017), soya bean (Wang et al., 2019) or Oilseed rape (Zhang et al., 2016). Most of these QTLs also map with root traits outlining the importance of roots and plant growth for Pi uptake. However, the identification of the causal genes underlying these QTLs remains mostly unachieved. So far, the only exception is the rice gene *PHOSPHORUS STARVATION TOLERANCE*

1 (*PSTOL1*) (Gamuyao et al., 2012). OsPSTOL1 has been identified within a major QTL enhancing rice growth in a highly Pi-deficient soil (Gamuyao et al., 2012). This QTL favours shallow rooting promoting topsoil foraging, where Pi usually concentrates. Interestingly, OsPSTOL1 is not present in modern varieties that are phosphorus-starvation-sensitive. Accordingly, its introgression significantly enhanced grain yield under phosphorus-deficiency, illustrating the negative impact of recent breeding strategies mostly based on high fertilizer level (Gamuyao et al., 2012). It has to be noticed that this gene promotes root exploration independently of Pi content, suggesting it may also improve nutrition for other limiting nutrients. *PSTOL1* has also been identified in other species such as sorghum, demonstrating the interest of translational biology approaches for breeders (Hufnagel et al., 2014).

Root plasticity is an important adaptive trait for Pi uptake. Accordingly, the search for increased PUE in Arabidopsis identified several genes affecting root development. They include a cell wall-targeted ferroxidase (*LPR1*) (Svistoonoff et al., 2007), a P5-type ATPase (*PDR2*) (Ticconi et al., 2004), the TF *SENSITIVE TO PROTON RHIZOTOXICITY 1* (*STOP1*) and its target *ALUMINIUM ACTIVATED MALATE TRANSPORTER 1* (*ALMT1*) (Balzergue et al., 2017; Reymond et al., 2006). Quantitative genetics and physiological analyses revealed the existence of natural variation for such traits in Arabidopsis, as well as in other species such as soybean, lupine and beans, offering opportunities for new breeding targets. Few species predominantly found among Australia flora (Lambers et al., 2013), where many native soils are highly Pi deficient and have developed a specific root anatomical adaptation named cluster roots (also known as 'proteoid' roots). It corresponds to specialized very short closely spaced lateral roots arranged in patches along the primary or lateral that release massive amounts of organic acid to solubilize Pi (Lambers et al., 2013). Recent studies have been undertaken in white lupine to identify the molecular bases and the functional coordination of these specific anatomical structures (Hufnagel et al., 2020). Deciphering the underlying mechanisms will open unprecedented perspectives to engineer Pi efficient crops. These species also lead to agronomical strategies of intercropping nonefficient with efficient crops, so that the accompanying crops will benefit from the presence of the efficient crops (Latati et al., 2014).

In many species, Pi starvation stimulates exudation of small organic acids (OA) such as malate and citrate. These OA solubilize Pi complexed with Al, Fe and Ca (Kochian et al., 2004), and it is well known that the massive exudation of these OA by proteoid roots is a mechanism to acquire phosphate in poor soils (Lambers et al., 2006). Malate and citrate are exuded by ALMT and MATE (Multidrug and toxic compound extrusion) transporters, respectively. In West African sorghum, SbMATE gene is associated with an improved grain yield QTL in Pi-poor soils (Carvalho et al., 2015; Leiser et al., 2014). Enhancing root exudation of these OA could be a way to improve Pi uptake. In barley, overexpression of the wheat TaALMT1 gene improves phosphate uptake efficiency in acidic soil (Delhaize et al., 2009), whereas overexpression of a bacterial citrate synthase in B. napus increased citrate synthesis and exudation and improves tolerance to Pi deficiency (Wang et al., 2013).

Another important parameter of root Pi uptake relies on microorganisms that can explore a large volume of soil and release organic acids to solubilize mineral phosphorus. Among them, the mycorrhizal symbiosis between plants and specific soil fungi is of particular interest and observed for ~80% of vascular plants. In such associations, the fungus will extract and provide Pi, and other nutrients such as N, to the plant and will receive carbohydrates in exchange (Wipf et al., 2019). Several agronomical companies provide mycorrhizal fungal solutions or soil enriched with mycorrhizal fungi to stimulate plant nutrition and growth (Basiru et al., 2021). However, such strategies are far from being universal. Their output depends on several parameters such as the crop species, the mycorrhiza partner and the local soil environment (Basiru et al., 2021). If technical advances have been made to increase inoculation efficiency at early stages of plant development for large-scale production using seed coating, it is currently difficult to control microorganism populations in field condition all along plant cycle due to the competitions with soil microflora (Hinsinger et al., 2011). Besides understanding microorganism population dynamics in soil, significant progress can still be made through the improved understanding of the critical steps of root/fungi interaction and to breed crops in which these interactions are optimized.

4.2 | Understanding and manipulating the Pi signalling pathways

Knowing that plants take up only ~20% of the applied Pi fertilizer, developing plants with an improved Pi use efficiency is of major importance. Indeed, most of the phosphate in the soil is trapped either under organic (due mostly to microorganisms' activities) or inorganic form (by clays or cations) making bioavailable Pi a scarce resource for plants. Solubilization of these pools of mineral and organic Pi is crucial but remains very difficult to reach for plants as the secretion of phosphatase (Wang et al., 2011) or organic acids by these organisms are important but present an action limited to the close vicinity of the roots. Association with endophytic fungi can also promote Pi recovery as illustrated by identification of endemic endophyte fungi in the natural Arabidopsis population (Hiruma et al., 2016). Even if they remain difficult to control, study of endophytes may provide an interesting way to improve Pi mobilization from soils which should not be neglected. Interestingly, the South-Western Australian flora provides an example where adaptation to very poor Pi soil results from powerful uptake capacities. The enhanced root Pi uptake predominantly results from a low capability to down-regulate high-affinity phosphate uptake system (Lambers et al., 2013). As a consequence, under abundant Pi supply, these species over accumulate Pi, resulting in toxic concentrations. It is therefore essential to identify all regulatory mechanisms controlling Pi uptake before overexpressing Pi transporters to avoid toxicity. In roots, Pi uptake is achieved through a suite of high-affinity transporters of the *PHOSPHATE TRANSPORTER 1* (*PHT1*) family and loaded into the xylem through the *PHOSPHATE 1* (*PHO1*) transporter (Muchhal et al., 1996; Poirier & Bucher, 2002). All these genes exhibit multiple layers of regulation, which may explain the general absence of success when attempts are made to manipulate (overexpress) directly Pi transporters (Rae et al., 2004). Nevertheless, the analyses of phosphorus use efficiency pinpoint phosphorus uptake as one of the important criteria distinguishing different coffee cultivars (Neto et al., 2016). The main regulation occurs at the transcriptional level (Kanno et al., 2016; Misson et al., 2005; Nussaume et al., 2011) and relies on the PHOSPHATE RESPONSE (PHR) master TF gene family (Bustos et al., 2010; Thibaud et al., 2010) and their regulators such as the SPX (named after the suppressor of yeast *gpa1* (Syg1), the yeast phosphatase 81 (Pho81) and the human xenotropic and polytropic retrovirus receptor 1 (Xpr1) domain protein family (Puga et al., 2014; Wild et al., 2016). The repression is a very rapid process, occurring within a few minutes following the uptake of phosphate (Hani et al., 2021). Several post-transcriptional levels of regulation of Pi transporters have also been identified (Bayle et al., 2011), including phosphorylation as reported in rice by the *CASEIN KINASE 2* (*CK2*) (Chen, Hu, et al., 2015; Chen, Wang, et al., 2015) or ubiquitination by the *PHOSPHATE 2* (*PHO2*) ubiquitin conjugase in *Arabidopsis* (Huang et al., 2013). Both regulate Pi uptake and translocation to shoots by modulating Pi transporter abundance at the plasma membrane (Aung et al., 2006). Similarly, also PHOSPHATE FACILITATOR 1 (PHF1), a protein involved in targeting the PHT1 transporters through the endoplasmic reticulum to the plasma membrane, regulates Pi uptake (Bayle et al., 2011; Chen et al., 2011; Gonzalez et al., 2005). Mutations in Pi transporters of the PHT1 family modify both high- and low-affinity responses to Pi (Ayadi et al., 2015). This suggests that PHT1 transporters can, according to Pi status, switch between two forms, but the underlying mechanisms remain so far unknown. Besides PHT1 regulation, the PHR/SPX signalling cascade also triggers a wide variety of mechanisms limiting Pi use by activating several metabolic shunts, such as the replacement of phospholipids by sulfo- and galactolipids and the secretion of enzymes including phosphatases to recover organic Pi present in the soil (Hurley et al., 2010). Taken together, these results illustrate that Pi homeostasis involves many players. Our current understanding of this complex regulatory network remains very fragmented, and further analyses are required to master these essential pathways for developing plants adapted to low Pi growth conditions. In addition, many studies report crosstalks between the metabolism of phosphate and other ions such as nitrogen, iron or zinc resulting most probably from adaptation to strong interactions taking place between Pi and metals within the soil and the plants (Guo et al., 2021; Hirsch et al., 2006). Taking into account, these multiple interactions, even if it is complex, may offer additional perspectives. This can be illustrated by new pathways recently discovered to be activated by plants to boost Pi accumulation in a zinc-dependent manner (Kisko et al., 2018).

5 | CONCLUDING REMARKS

The examples reported in the review illustrate the recent advances in understanding the physiological and molecular bases of how plants respond to their environment. Moreover, they provide opportunities for improving and stabilizing crop production, contributing to future food security (Figure 1). They also highlight several future directions that will be further investigated in the CropBooster-P project. Firstly, even if tremendous advances have been made in deciphering the bases of adaptive responses, the examples presented in this review demonstrate that basic research remains essential. For instance, knowledge on the molecular bases of the regulation of water transport at the whole plant level and their response to environmental cues, as well as the underlying mechanisms governing plant adaptation to heat stress, remains limited. Secondly, it is important to note that many studies have been done in model species or a limited number of crops and/or under specific and controlled conditions. In the future, it will be crucial to extend this knowledge to a wider range of crops which are grown in field conditions. Indeed, although Pi, NO_3^- and NH_4^+, transporter families have been identified in all species, their regulation can differ significantly between species and appears to be strongly dependent on the age of the plant and the environment (Nacry et al., 2013). Thirdly, future research

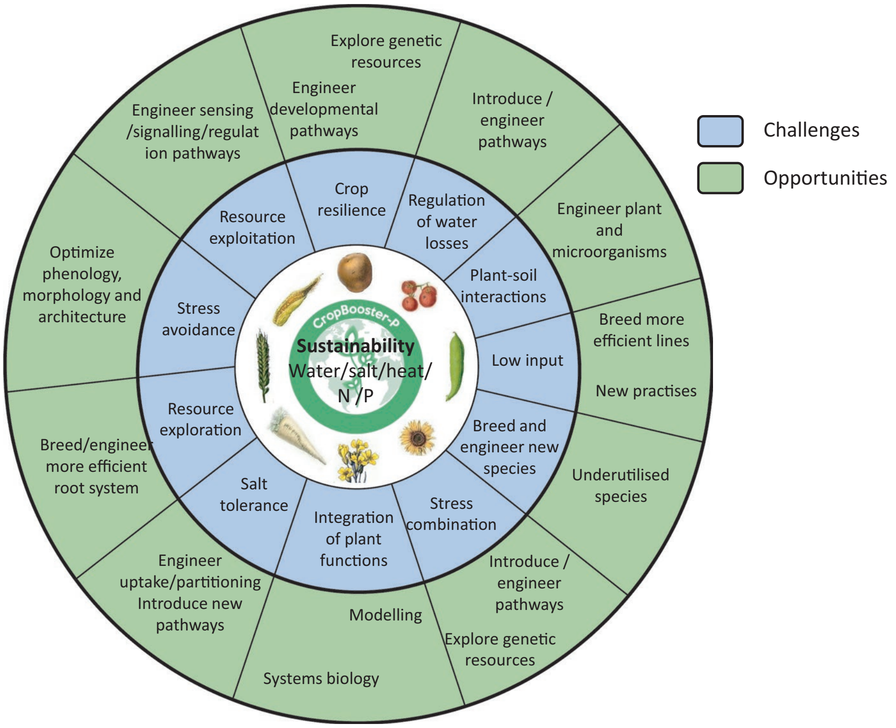

FIGURE 1 Prospects to improve crop resilience and sustainability of crop production. It includes challenges (blue) and opportunities (green) with the aim to prepare a roadmap for the development of improved crops in the frame of the CropBooster-P project

projects will only be efficient if integrated approaches are being used. For instance, drought and heat stress are strongly interlinked as drought stress often occurs when temperatures are high. Water deficit reduces stomatal conductance and transpiration enhancing heat stress as leaf temperature rises. Under field conditions, the combined effects on plant growth and performance are higher than when considered individually (Dreesen et al., 2012; Zandalinas et al., 2016). Similarly, as underlined above, NO_3^-, phosphate and iron uptake are tightly interconnected and need to be considered together (Kisko et al., 2018; Thibaud et al., 2010). Fourthly, strategies to significantly enhance crop resilience and sustainability will rely on systems biology approaches involving physiologists, geneticists, breeders, agronomists and modellers. Indeed, it is well known that NO_3^- is not only a major N source, but also a signal molecule. Accordingly, NO_3^- signalling pathways regulate multiple metabolic pathways, as well as several developmental processes such as root development, seed dormancy and flowering time. Modifying NO_3^- uptake and signalling may thus trigger coordinated changes in various synergistic processes in an integrated response that may result in adverse effects that could strongly impact other desirable traits, such as heat or drought stress tolerance. Fifthly, development and deployment of new technologies, in particular in field conditions, and big data management will be essential. The different examples explored in this review underlined the central role of roots, the hidden half of the plant. Indeed, roots control water and nutrient uptake and regulation of their development governs soil foraging for resources. Roots are also in close contact with the soil microbiota, and the impact of microorganisms on plant development and resilience remains still largely unknown. A better understanding of root development, functioning and plasticity in model species and crops in a wide range of field conditions and the integration of massive data will be crucial to breed for more tolerant and resilient crops. To reach this goal, it will also be necessary to develop new phenotyping and functional phenotyping methodologies under field conditions. Finally, addressing crops' adaptation to climate change and low inputs' agriculture requires integration of genetic resources and emerging technologies such as genome editing or synthetic biology to capture, combine and exploit new and/or complex traits. This may also rely on the use of underutilized crops and acclimation of new species that are more resilient to fluctuating environments or used to develop innovative culture practices such as intercropping and agroforestry where associated species provide nutrients, deep water or shade.

To meet the future global needs, it will also be crucial that the approaches to improve sustainability of crop production and crop resilience are complemented by advances to increase plant yield (LINK TO YIELD REVIEW), while promoting the crops' nutritional quality (LINK TO NUTRITIONAL QUALITY REVIEW).

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