



Genome-Wide Association Studies and Genomic Selection for Nutrient Use Efficiency in Cereals

5

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Abstract

Cereals are essential food crops ensuring global food and nutritional security by providing more than 60% of global calories requirement. However, cereal production is under threat owing to various climate change-mediated abiotic and biotic stresses. Additionally, the low and injudicious usage of nutrients is a major impediment to achieve nutrient use efficiency in cereals. Among essential nutrients, nitrogen (N), phosphorus (P) and potassium (K) are the major nutrients required in greater amounts for the proper growth and development of crops. Besides better agronomic practices, the development of cereal cultivars with genetically enhanced nutrient use efficiency is the most sustainable approach to improve NUE and reduce the cost of cultivation and environmental pollution. The availability of complete genome sequences in cereal crops has greatly contributed to enormous molecular markers and high-density linkage maps to implement the next-generation breeding approaches to enhance the genetic gain through nutrient

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161

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use efficiency. Among the various genetic tools in crops, genome-wide association studies (GWAS) and genomic selection (GS) can improve complex traits like nutrient use efficiency traits in cereals by altering functional adaptive traits. Further, the developments in phenotyping approaches coupled with GS and GWAS revealed various candidate genes for nutrient use efficient adaptive traits and their possible mechanisms in enhancing the major nutrient use efficiency in cereals. Here, we presented key updates on the application and utility of GS and GWAS in cereals to improve the N, P and K use efficiency in cereals.

Keywords

Nutrient use efficiency (NUE) · Genetic gain · Genomic selection · Genome-wide association analysis Cereals

5.1 Introduction

Cereals play a central role in providing major food calories to the human population. Thus, improving cereal yield to fulfil the demand of the increasing human population is becoming a challenging task. Global cereal production is determined by various genetic, edaphic and environmental factors. Among various crop growth determinants, nutrients are the important factors influencing grain yield and the nutritional profile of cereals. Nitrogen (N), phosphorus (P) and potassium (K) are the important key nutrients capable of producing major impacts on cereal production and the most prominent external inputs in modern agriculture. These major nutrients, viz. N, P and K, are the essential components of protein, nucleic acid, chlorophyll, cell wall, energy carriers, osmoregulation, photosynthesis and several secondary metabolites (Shrivastav et al. 2020; Sanchez-Bragado et al. 2017). The external application of NPK fertilizers has significantly increased the global cereals' yields and heralded the green revolution in Southeast Asia. The FAO reported the huge rise in global demand for NPK from 186,625 thousand tonnes (2016) to 199,006 thousand tonnes (2019) (FAO 2016). However, the improper and non-judicious application of major fertilizers results in lower NUE and environmental pollutions (Wuebbles 2009; Pingali 2012; Ng et al. 2016). Though the use of synthetic fertilizers appreciably improves crop performance in terms of grain yield, plants could be able to absorb only 30–40% of the externally applied fertilizers (Curci et al. 2017).

The nitrogen utilization efficiency (NtUtE) is only 40% out of 94 million tonnes of externally applied N fertilizers (Plett et al. 2018). Further, high application of N fertilizers coupled with improper agronomic practices, viz. wrong irrigation, ploughing, fertilizer application patterns, etc., is increasing the N losses through denitrification/volatilization, leaching and immobilization and creating a global hazard to the environment. Insufficient application of N reduces the crop yield, whereas excess application expands the vegetative growth phase and susceptibility

to pests and diseases and creates several environmental pollutions (Dogan and Bilgili 2010; Liu and Shi 2013).

The P is the next important major nutrient after N, and any deficiency severely affects the crop performance (Hussain et al. 2008; Ziadi et al. 2008; Haileselassie et al. 2014; Jeong et al. 2017). Soils with the highest P fixation show high P deficiency and reduced crop production. The tropical regions are home to approximately 1018 million hectares (ha) of land with problems like P fixation and P deficiency (Sanchez and Logan 1992). Nearly 67% of world agricultural land is deficient (Batjes 1997; Hinsinger 2001). The manufacture of phosphorus mostly depends on rock phosphate, the common and primary non-renewable source of P. The P fertilizers' prices are significantly inflated due to the possibility of rock phosphate depletion in the preceding 50 to 100 years (Cordell et al. 2009). The P availability to plants is influenced by various soil factors, viz. pH, alkalinity, acidity, etc. (Lindsay et al. 1989; Marschner et al. 1986). Besides immobile nature in soil, the P losses occur in sandy soils, soils with high organic content and soils with overapplied P fertilizers. The lost P in the environment is detrimental to the aquatic ecosystems and results in aquatic blooms (Sims et al. 1998; Ashley et al. 2011). The third most major nutrient is K and plays a prominent role in osmoregulation, protein metabolism, enzyme activity, photosynthesis and photoregulation (Gattward et al. 2012; Hastings and Gutknecht 1978; Schachtman and Shin 2007; Safdar et al. 2020). Additionally, K is also known to influence NtUE, tolerance to pests and diseases and product quality (Brar et al. 2011; Shabala and Pottosin 2014). The neglected K management is one of the primary reasons for low productivity in the agricultural production systems of the developing world.

To maximize the genetic gain in cereals and to discourage the high-input agriculture system and minimize collateral damage to the environment and society, nutrient use efficiency (NUE) of N, P and K remains one of the crucial strategies. Several classical and modern breeding approaches have been devoted to improving the N, P and K use efficiency in various cereals. Here, we have briefly discussed how plants acquire N, P and K nutrients at the molecular level and how the use efficiency of nutrients can be maximized by deploying molecular tools like genome-wide association mapping and genomic selection with particular reference to major cereals. Several techniques have been proposed at the agronomic and physiological levels to improve high NUE. In cereals, exploring genetic variability across the various crop gene pools could be one of the efficient and sustainable approaches to improve the nutrient use efficiency in addition to minimizing the overusage of fertilizers that cause environmental pollution. Multiple genetic factors influence the NUE, and the large genotype by environment interaction makes genetic dissection quite challenging. Several genes and QTLs have been elucidated based on classical genetics and bi-parental mapping populations in various cereal crops. To understand NUE, the availability of high-throughput molecular markers, especially single nucleotide polymorphisms (SNPs), can further shed light on the underlying candidate gene (s)/QTLs controlling NUE across the whole genome level. Thus, these SNP markers could greatly facilitate practising genomic selection to select high N, P and K use efficient breeding lines in cereal crops.

Likewise, breakthroughs in functional genomics and the availability of complete genome sequences of cereal crops have greatly allowed us to pinpoint the candidate gene(s) and their possible function controlling NUE. However, phenotyping of this trait remains a major hurdle in improving high NUE in crops. Thus, emerging high-throughput phenotyping and machine learning approaches could increase our understanding of NUE at the phenotypic level. We have also discussed the scope of employing other powerful breeding techniques like genomic selection, genome-wide association mapping and CRISPR/Cas9-based genome editing technology to improve the NUE with suitable examples.

5.2 Functional Adaptive Traits for Nutrient Use Efficiency in Cereals

Understanding the traits and metabolic and physiological processes governing NUE, resulting in improvement in yield by any increment in nitrogen, phosphorus and potassium application or sustaining its productivity in low or moderate nutrient stress conditions, is vital to breed plants for nutrient use efficiency or nutrient stress-tolerant lines. Functional traits that include morphological, biochemical, physiological, structural, phenological or behavioural traits and their response to the environment and effects on the ecosystem properties should be given thrust (Violle et al. 2007). These are of two types, i.e. effect traits and response traits. Effect traits are those that have an impact on the ecosystem and the services or disservices that it provides to human societies. Response traits are the ones that impact the colonization, flourishing and spread of a species and its sustainment in the changing environment. Some of the characters can act as both effect and response traits. Functional adaptive traits are the traits that help in the survival of species in the target environment. Various functional adaptive traits are found in the cereals, such as relative growth rate, germination rate, leaf mass index, frost tolerance, potential photosynthetic rate, etc., and several are associated with the NUE (Youngquist et al. 1992; Maranville and Madhavan 2002; Jia et al. 2008; Ning et al. 2013; Wang et al. 2017a, b; Silva et al. 2016; Wang et al. 2019b; Sharma et al. 2021). Nutrient usage is divided into several stages, for instance, in the case of N, uptake phase, reduction of N into usable forms, absorption into different components of biomolecules and finally reallocation from different tissues to the reproductive part (Masclaux-Daubresse et al. 2010). Similar processes are involved in P and K use in plants. The various target phenotypes and physio-biochemical traits that are used to enhance the major nutrient use efficiency in cereals are summarized in Table 5.1.

Table 5.1 Various morphological, physiological and biochemical adaptive traits for major nutrient use efficiency in cereals

Stages	Nitrogen use efficiency	Shoot-specific target traits	Reference
Morphological traits	Shoot and leaf traits	<ul style="list-style-type: none"> • Days to germination • Green leaf number/plant • Yellow leaf number/plant • Total leaf number/plant • Number of senesced and green leaves • Number of purple leaves • Days to onset of flowering • Days to 50% flowering • Anthesis and silking interval • Stem thickness • Stalk diameter • Plant height • Shoot length • Biomass (dry and fresh) • Total seeds/panicle or ear • Per cent unfilled and filled ears/spikelet • Grain weight • Harvest index 	Andresen et al. (2016) Bruen and Struik (2017) Ciampitti and Vyn (2012) Ehdaie et al. (2010) Sharma et al. (2021) Guttieri et al. (2017) Hirel et al. (2001) Maranville and Madhavan (2002) Tollenaar and Lee (2011) Wang et al. (2019a)
	Root traits	<ul style="list-style-type: none"> • Root length • Root biomass • Root density • Number of roots (seminal) • Fine hairs in root • Lateral root count 	
Biochemical and physiological traits	Shoot and leaf traits	<ul style="list-style-type: none"> • Stay-green trait of leaf • Chlorophyll content • Leaf area index • Leaf photosynthetic rate • N/P/K uptake • Leaf area index (LAI) • Carbon exchange rate • Carbon isotope ratio • Assimilation efficiency indices • NADP malic enzyme activity • Total soluble protein • RuBisCO activity • Glutamine synthetase activity • Nitrate reductase activity • PEPCase activity • Nitrogen internal efficiency • Nitrogen response efficiency 	

(continued)

Table 5.1 (continued)

Stages	Nitrogen use efficiency	Shoot-specific target traits	Reference
		<ul style="list-style-type: none"> • Nitrogen harvest index • Nitrogen remobilization ratio • Nitrogen contribution ratio • Photosynthetic nutrient use efficiency • Phosphorus concentration in stems and leaves • Phosphorus concentration in grain • Phosphorus harvest index (%) • Phosphorus acquisition efficiency (PAE) • Phosphorus internal efficiency (PIE) • Phosphorus biological ratio (PEBR) • K concentration in stems and leaves • K concentration in grain • K harvest index (%) • K uptake efficiency (KUpE) • K utilization efficiency (KUtE) 	
	Root	<ul style="list-style-type: none"> • Hydroponic root exudate estimation 	

5.2.1 Types of Traits Associated with Nitrogen Use Efficiency in Cereals

5.2.1.1 Morphological Traits Associated with Nitrogen Use Efficiency

NtUE is usually defined as the uptake, utilization and physiological efficiency of N by the plants. As far as agronomical efficiency is concerned, the yield increment per unit of N applied or the output-to-input ratio is the main criteria for NtUE (Raghuram and Sharma 2019). There are different N-responsive traits in the plants like germination percentage, green leaf number at the vegetative and flowering stages, yellow leaf number at the vegetative and flowering stages, total leaf number at the vegetative and flowering stage, leaf width, stem thickness, shoot length before and after harvest, specific leaf area, leaf life span, leaf senescence, fresh and dry biomass of root and shoot, root length, total plant height, days to flowering, unfilled grain weight, filled grain weight, panicle weight, filled grain percentage, harvest index, root absorption capacity, number of ears/plant, number of grains/ear, thousand grain weight, grain yield/plant, weight of panicle remains, etc. (Lammerts van Bueren and Struik 2017; Sharma et al. 2021). Decreased grain yield up to 37% in low nitrogen level in

comparison to high nitrogen level was observed in experiments conducted by Presterl et al. (2003) in European maize. Reduced kernel abortion, anthesis-silking interval and ear number per plant were found to be stress indicators associated with N use efficiency (Gallais and Coque 2005; Geiger 2009). A strong genetic correlation between the plant height and flowering days with N use efficiency was found in hard winter wheat (Guttieri et al. 2017). Further, the studies showed that under limited N, the larger root system of efficient genotypes showed higher N uptake and did not necessarily decrease significant grain yield in winter wheat (Ehdaie et al. 2010; Andresen et al. 2016). Similarly, the wheat genotypes grown in deep tube rhizotrons under limited N showed significant differences in the spatial distribution of root architecture and root biomass, suggesting that the improved root growth in the initial growth phase adapts to the N starvation better (Andresen et al. 2016).

5.2.1.2 Physiological and Biochemical Traits Affecting Nitrogen Use Efficiency

Various N-responsive physiological traits were studied by various researchers, such as leaf chlorophyll concentration, carbon exchange rates (CER), PEPCase activity, NADP-malic enzyme activity, RuBisCO activity, photosynthesis rate, plant total N concentration, plant total protein content, leaf N content, etc. (Maranville and Madhavan 2002; Wang et al. 2019a). N uptake efficiency (NtUpE) or N recovery efficiency (NtRE) and N utilization efficiency (NtUtE) or nitrogen internal efficiency (NtIE) are the components contributing to N use efficiency. Agronomically, NtUE is the product of NtRE and NtIE, i.e. $NtUE = NtRE \times NtIE$ (Moll et al. 1982; Ciampitti and Vyn 2012). NtRE is important in high N supply environments, whereas NtIE is imperative in low N environments. NtUpE is the amount of N taken up from soil which usually depends on the root system architecture (RSA) and its capacity to mine (Eghball and Maranville 1993). According to Moll et al. (1982), NtUtE is the grain yield produced per unit of plant N. Maranville et al. (1980) believed both grain and forage produced per unit of plant N is important in NtIE. Ciampitti and Vyn (2011) and Ciampitti et al. (2013) explained other parameters important in NtUE estimations such as N harvest index (NtHI), N remobilization ratio (NtRR) and N contribution ratio (NtCR).

Wang et al. (2019a) conducted an experiment in two commercial hybrids and their parents in maize and concluded that 52% of the total variation was accounted by NtIE and said NtUE is ascribed by a pre-anthesis accumulation of N results in the faster appearance of the leaves with maximum leaf area index, PtNUE and faster remobilization of N from leaves and stalk. However, the stay-green trait and reduced grain N concentration were also reported by Ciampitti and Vyn (2012). From this, it could be understood that N utilization efficiency/NtIE decreases the nitrogen in grains to maintain the yield in N stress conditions. Physiological adaptation in sorghum for NtUE was studied by Maranville and Madhavan (2002) by comparing two high NU efficient Chinese lines and two less NU efficient US lines and suggested that PEPCase and enzymes that are connected with phosphoenolpyruvate production play the roles in sustaining photosynthetic efficiency under N stress conditions. In maize, NtUE was increased by selecting genotypes with a higher

NO_3^- storing capacity in leaves, leaf longevity or stay-green trait and prolonged reproductive phase N accumulation (Hirel et al. 2001; Tollenaar and Lee 2011). Various biochemical traits such as assimilation efficiency indices (ACi), glutamine synthetase (GS), nitrate reductase (NR) and protein content in grain and leaf were found to be important in NtUE (Maranville and Madhavan 2002; Vijayalakshmi et al. 2015). Maranville and Madhavan (2002) confirmed with their experiment that high CO_2 assimilation is linked to higher biomass production in low leaf N conditions in sorghum. In aromatic rice genotypes, the GS activity was more in low N conditions and high NU efficient lines, whereas NR activity was more in low NtUE genotypes (Vijayalakshmi et al. 2015). In addition, protein content in grain was found to decrease in low N conditions. Osman et al. (2012) insisted on improving the N uptake efficiency to maintain the grain nitrogen in bread wheat as it is very crucial to the protein quality of bread. Increasing N application enhanced grain protein content and protein yield in six spring wheat genotypes (Gauer et al. 1992). Tiong et al. (2021) utilized the genetically modified rice lines overexpressing *alanine aminotransferase* for studying the changes in pathways for NtUE, and it was found that carbon metabolites, especially those associated with glycolysis and TCA (tricarboxylic acid) cycle, were significantly changed in roots suggesting high metabolic turnover and its upregulation in low N stress conditions. This could result in better energy production and higher N assimilation and, in turn, enhance the biomass. Phytohormonal and secondary metabolite changes are also potential mechanisms in the high NtUE phenotype.

5.2.2 Types of Traits Associated with Phosphorus Use Efficiency in Cereals

5.2.2.1 Morphological Traits Associated with Phosphorus Use Efficiency

Root traits are considered important to scavenge phosphorus from soil. Root characteristics such as more adventitious roots and lateral root spreads, smaller root diameter, shallower basal roots, good root biomass and longer and denser root hair are important to improve the P uptake in soil (Wang et al. 2004; Yan et al. 2004; Lynch 2007; Richardson et al. 2011; Silva et al. 2016). Increased axial root length without lateral root branching is seen in maize as exploratory behaviour (Richardson et al. 2011). Topsoil is richer in P availability; hence, shallower basal root and increased root density in upper layers are well-balanced adaptive characteristics for high PUE. Screening of wheat genotypes for PUE showed an increased biomass and root/shoot ratio in P efficient genotype compared to inefficient genotype (Yan et al. 2010). Traits which originate from the stem or from other tissues, such as crown root formation in maize, can also be helpful for phosphorus uptake (Ochoa et al. 2006). Along with the above-mentioned traits, root and shoot fresh and dry weight, tiller numbers per plant and root to shoot biomass are notable traits for PUE in cereals. Li et al. (2021) reported a decline in PUE and phosphorus acquisition efficiency (PAE) from founder to elite flints and confirmed the shorter root hair and smaller root system at low P as beneficial traits.

5.2.2.2 Physiological and Biochemical Traits Associated with Phosphorus Use Efficiency

Phosphorus use efficiency is divided into two components PUE or PAE and phosphorus internal efficiency (PIE). Root exudates play a role in improving the PAE. These exudates comprise protons and organic acids such as citrate, malate oxalate, etc. Acid phosphatases and ribonucleases upon exudation are known to release fixed P in soil (Vance et al. 2003). P transporters located in cell membranes are also important in P acquisition. PIE depends on the optimal allocation of P inside the plant system. In cells, P is present in two forms, i.e. free inorganic orthophosphate and organic phosphate esters. Inorganic phosphate (Pi) is influenced by P supply (White and Hammond 2008). Excess Pi is stored in vacuoles which will be utilized in P-deprived conditions (Mimura et al. 1990). Organic phosphate is present in nucleic acids, phospholipids, metabolites and proteins. Large P concentration in the seed is not suitable for monogastric animals as their intestine cannot absorb the phytate form of P present in seeds, and it goes to the environment and results in pollution. Seed P concentration is decreased gradually upon breeding for high-yielding varieties, but this will affect the seed vigour in order to compensate that seeds can be coated with P fertilizer (Veneklaas et al. 2012). Remobilizing the P from senescing plants to the growing plant parts and grains is also an important criterion to improve the internal P use efficiency. Phospholipids present in the cell membrane can be bred to be replaced by non-phosphorus compounds such as sulpholipids and galactolipids. It can be replaced either constitutively or in response to P deficiency (Lambers et al. 2012). Cell walls can be adapted by synthesizing P-free polysaccharides such as cellulose (Rao and Terry 1995). Wang et al. (2017a) concluded in their experiment in rice that low P in straw and better grain yield indicated improved P translocation and translocation efficiency of P. Gill et al. (2004) screened 30 spring wheat varieties for their P uptake and use efficiency and could identify high grain yield and high P uptake genotypes (WH711 and PBW343) and high grain yield and low P uptake varieties (Raj3765 and WH283).

5.2.3 Types of Traits Associated with Potassium Use Efficiency in Cereals

5.2.3.1 Morphological Traits Associated with Potassium Use Efficiency

Morphological traits, especially root traits, are important to acquire soil potassium at low K^+ concentration and proliferate into deeper layers in search of K^+ and its ability to extract non-exchangeable K^+ (White et al. 2013; Steingrobe and Claassen 2000; Wang et al. 2011). A larger root system and increased root density help in greater K^+ acquisition (Zörb et al. 2014). The uptake increases in roots with the larger specific surface area, which is achieved in roots with more branches and finer root hairs (White et al. 2013). The deeper root system helps in K^+ uptake from subsoils (Ehdaie et al. 2010). Samal et al. (2010) reported that wheat acquired more K^+ due to greater root length to shoot length. Grain yield is also known to increase in response to K^+ fertigation in maize (Ebelhar and Varsa 2000). Part of yield increase may be

accounted for improved stalk strength (reduced lodging), particularly when high K^+ and N fertilizers are applied (Welch and Flannery 1985). Similar results were reported in the wheat crop (Beaton and Sekhon 1985; Haeder and Beringer 1981). Jan et al. (2018) reported a significant effect of potassium on crop phenology, growth and yield traits. In rice, Jia et al. (2008) observed that K^+ efficient lines had more fine roots and root surface compared to inefficient lines. Larger root/shoot biomass ratios in rapidly growing crops have greater K^+ demand, and they are often met by greater K uptake capacities. Roots of cereals possess larger uptake capacities (Pettersson and Jensén 1983).

5.2.3.2 Physiological and Biochemical Traits Associated with Potassium Use Efficiency

In agronomy terms, potassium use efficiency (KUE) is the grain yield produced per unit of available K^+ , which is divided into components K uptake efficiency (KUpE) and K utilization efficiency (KUtE). KUE is also measured in terms of the response of grain yield to K availability, tissue K^+ concentration to available K^+ (White 2013) and the response of yield to plant K^+ content. Physiological K^+ requirement in plant accomplishes 90% of its growth and growth rate at critical tissue K^+ concentration (White 2013). Physiological KUtE can be improved by the replacement of vacuolar K^+ with other solutes and increasing remobilization of K from older leaves to other growing and younger parts. Physiological K^+ efficiency is also depending on K^+ transport channels. Many transport proteins are involved in various cellular membranes. These transporters are precisely regulated to modulate the K^+ homeostasis in cellular compartments (White and Karley 2010; Véry et al. 2014). Root exudates also play a role in the K^+ uptake capacities of species. Carboxylates such as citrate, malate and oxalate can dissolve feldspars and micas to release potassium (Marchi et al. 2012). Root-induced acidification of soil releases non-exchangeable K in soil (Giles et al. 2017). All these vary significantly between species and genotypes within species. Potassium utilization efficiency is significantly correlated with K^+ translocation ability, which in turn affects the grain yield, biomass production in seedling tillering stages and harvest index in rice (Yang et al. 2004). The malic acid exudate was increased upon K^+ supply as observed in maize by Krafczyk et al. (1984). The experiment in maize comparing the accumulation and remobilization of nutrients (NPK) confirmed that new varieties took up more N, P and K during the post-silking stage and remobilized well to the grain in comparison to old varieties (Ning et al. 2013).

5.3 Strategies to Improve Nutrient Use Efficiency in Cereals

The demand for food is increasing every year because of the growing population and lower rate of crop yield per unit area. Repeated cropping of high-yielding varieties takes up excess nutrients from the soil, resulting in poor fertility, and will create environmental stress in soil. The major challenge of feeding the population can be achieved by increasing the production per unit area and maintaining soil health (Atiq

et al. 2017; Hussain et al. 2002; Leghari et al. 2016). Many a time, the availability of the nutrient is the limiting factor for the yield; on the contrary, in the high input agriculture system, farmers apply a higher dose of chemical fertilizers. Excess chemical fertilizers created a significant environmental concern in several aspects (Vitousek et al. 2009). Compared to biotic and abiotic stresses, nutrient management is the least attended aspect in plant breeding, even though it was well established that nutrient management contributes to the higher productivity of a cultivar.

NUE refers to production of yield per unit of nutrient or fertilizers applied to field (Ortiz-Monasterio et al. 2001). It comprises two issues: 1) the ability of crop to uptake the nutrients from the soil through the roots and 2) the ability to mobilize these nutrients towards an increased yield (McDonald et al. 2013). The NUE is a complex phenomenon, where it is affected by several environmental factors, rhizosphere condition, plant root architecture, genetic makeup and physio-biochemical and biological condition of the plant. Across the world, many experiments were performed on the effects of fertilizers on yield and soil fertility (Berzsenyi et al. 2000; Zhang et al. 2009; Duncan et al. 2018; Gulser et al. 2019).

Despite significant investments in NUE research, very few crop varieties have been released with nutrient use efficiency. Because of the NUE-associated phenological and physiological trait complexity, there are no single or few traits for assessing NUE. Therefore, there is a need to select several NUE-related traits and assess the cultivars with respect to NUE. Though conventional breeding strategies to enhance NUE were considerably applied in the important crops, like rice, maize and wheat, very few efforts have been attempted to explore the candidate genes associated with NUE characterization and their association with NUE phenotypes in cereals.

5.3.1 Improving Root Architecture

The RSA contribute significantly to crop productivity, since roots extract essential nutrients from the soil. The importance of root morphology parameters in the uptake of a variety of nutrients was indicated by the mechanistic mathematical models based on ion uptake, soil nutrient supply and root morphology (Barber and Cushman 1981; Barber and Silverbush 1984). Therefore, better root growth is considered as prerequisite for healthy plant growth. Differential transcriptome expression analysis of roots in the low and high NUE crop gives an idea about the root architecture. Lateral growth of the root in cereals enhanced the NUE, where overexpression of *OsNPF8.20(OsPTR9)*, a lateral root formation promoting gene, resulted in higher lateral root formation and efficient N uptake and, as a result, increased tiller and effective panicle number and grain yield (Fang et al. 2013). Therefore, targeting various attributes of RSA is one of the major strategies in NUE breeding of cereals.

5.3.2 Genetics of Root-Microbe Interaction

Nutrient uptake is determined by root growth and the bioavailability of nutrients in the rhizosphere. When different NUE responding lines were selected for studying microbial communities in their rhizosphere, different microbial communities and metabolic pathways were observed. Different transcriptional activities like N mineralization, ammonification, nitrification and de-nitrification were evident along with differential expression of subunits of the same genes, denoting that the two plants with different NUE not only were chosen for particular microbial community in rhizosphere but also induced the gene expression (Pathan et al. 2018). Dual transcriptome analysis of the rhizosphere gives a clear picture of gene expression and pathways. A transcription profile will help to identify genes involved in nutrient mineralization, proper interaction, suction and assimilation of the nutrients. Many plant growth-promoting bacteria (PGPB) improve root growth; however, their effectiveness could be determined by the nutrient status in rhizosphere. The attraction of the microbial biome depends on the root exudates. Therefore, modifying the cereals' root exudates could change the nutrient uptake and is expected to enhance NUE. The cereal genotypes showing efficient root exudates to facilitate the colonization of NPK mobilizing microbes could be an added strategy to improve NUE in cereals.

5.3.3 Identification of Candidate Genes Related to Nutrient Use Efficiency

Breeding efforts are to be made to enhance the NUE of crops specifically to obtain higher yields under the low nutrient status of the soil, since there is no clear single phenotypic characteristic or any single gene/QTL for differentiating high or low NUE or that exclusively increases the grain yield. Nevertheless, previous QTL studies identified genomic regions for grain quality- and quantity-related traits, i.e. ear leaf area (ELA), plant height (PHT), grain yield (14% moisture) per plant (GYP), number of ears per plant (EPP) and number of kernels per ear (NKE) and kernel weight (KWT) (Agrama et al. 1999). These traits showed comparatively higher heritability correlation >0.5 under different N levels. With respect to P and K, there are no clearly defined phenotypic traits as of now. Since there are very few phenotypic markers, a tremendous opportunity is available to utilize genetic markers like SNPs, ISSRs, SSRs, etc. Once nutrient is taken up by the plant, there will be switching on of different pathways till it reaches the yield/grain formation stage. Recent innovations in the next-generation sequencing (NGS) platforms made them a highly reliable tool in understanding the functional genomics of the low and high NUE crops. Application of different 'omics' could hasten the current studies on NUE. Based on the previous studies, genes related to *glutamate-pyruvate transaminase (GPT)*, *glutamate-glyoxylate aminotransferase (GGT)*, *high-affinity nitrate transporters (NRT2)* and the associated partner protein (*NAR2*)

families were considered as candidate genes for N use efficiency (Araki and Hasegawa 2006; Cai et al. 2008; Feng et al. 2011; Hu et al. 2015).

5.3.4 Genetic Engineering to Increase Nutrient Use Efficiency

Several NUE-related candidate genes identified can be exploited either through a transgenic approach or through gene editing to rebuild the metabolic pathway or increase the specific gene expression to increase the NUE. In rice, few members of NRT1/PTR, 4 NRT2 and 2 NAR2 signal transporter gene families have been functionally characterized. Signal transporter gene expression at the roots enhanced the yield by 30–40% compared to their mutant (Sánchez-Calderón et al. 2006). The comparative genomic study is helpful to explore more genes in the other cereals too. In wheat, *alanine aminotransferase* gene transferred from barley enhanced the N use efficiency in greenhouse conditions (Ahmed et al. 2020). Targeting primary assimilation was also found beneficial and proven that overexpression of *cytosolic glutamine synthetase (GS)* isoform in maize increased the kernel number and grain yield by nearly 30% against control type (Martin et al. 2006). In rice, various transporter gene families for the same nutrient were discovered, but allelic variation altered uptake kinetics of nitrate transporter, and differential uptake capability (Hu et al. 2015) between two subspecies was observed. In such cases, gene editing is the best tool to modify the targeted genes.

Only N is the most abundantly studied nutrient in model plants. Still, there is scope to understand and identify NUE candidate genes and trait selection for phenotyping for other nutrients. Along with genetic improvement, good agronomic practices can effectively aid in exploiting the full genetic potential of the cultivar. It is always advocated to conserve the optimum rhizosphere conditions such as pH, temperature, water level, healthy synergetic microbial load and soil aeration.

5.4 Genetic Resources for Genome-Wide Association Analysis and Genomic Selection in Cereals for Nutrient Use Efficiency

Cereals like rice, wheat and maize are the principal sources of food and nutrition to the human population. With the rising global population, there is a demand for adequate production of food grains. Hence, there is a need to improve crop yields through the efficient use of resources, including NPK fertilizers, to achieve the sustainability of food production. Crop yield can be improved through the breeding cultivars that high yields high with limited fertilizer inputs through utilization of cereal genetic resources. The genetic variability in the elite germplasm is essential to improve quantitative traits, including NUE. Decades of breeding cereals for high-yield and high-input agriculture have developed the cultivars poorly adapted to low nutrient availability. Interestingly, there are few reports on modern nutrient-responsive germplasm in crops like wheat and maize (Hirel et al. 2007; Moose

and Below 2009). Therefore, it shows the presence of genetic variation for NPK use efficiency and component traits to explore (Garnett et al. 2015; van de Wiel et al. 2016; Maharajan et al. 2021). Several nutrient use efficient genotypes were identified in major cereals. Recently, Jia et al. (2020) reported four rice lines, viz. 99–28, Shennong 315, Teyou 2 and Xindao 41, for NtUE through screening at four levels of N supply 0, 104, 207 and 311 kg/ha. Similar, more than 100 rice landraces given relatively higher yield under treatment of no N application. This study suggests the importance of land races as source of breeding material for NUE in cereals (Rao et al. 2018).

As compared to N, quite few reports are available on the screening of cereal germplasm for P and K stress owing to difficulty in creation of P and K sick plots. In rice, several lines were reported for PUE, viz. Wazuhophek (Swamy et al. 2019), ULR026, ULR031, ULR124, ULR145, ULR180, ULR183, ULR185, ULR186, ULR213, ULR260 and ULR305 (Chankaew et al. 2019). Similarly, in the case of wheat, Nisar et al. (2016) reported NR-397, NR-379, NR-390, NR-403, NR-401, NR-378 and NR-404 as the most efficient lines. Additionally, Hari-Gowthem et al. (2019) reported wheat lines pau16059, pau16063, pau16065, pau16066 and pau16067 for enhanced PUE. Further, heritable variations for NUE in exotic germplasm and populations evolved under low input agricultural systems may also serve as treasures of NUE genes. Unfortunately, very limited efforts were directed in the utilization of germplasm of exotic and low input agricultural systems in the evaluation and improvement of NUE or component traits, owing to lack of knowledge base and difficulty in phenotyping of NUE phenologies (Ranjan and Yadav 2019).

The variation between genotypes can be used to select superior genotypes and/or genes that play an important role in NUE (Mohammed 2018). Nutrient uptake mainly depends on the genotype and the interaction between genotype and the environment resulting in significant differences in nutrient uptake and utilization efficiency and composition (Zhang et al. 2020). Using genotypes with more efficient nutrient absorption efficiency at low nutrient soil leads to result in increased crop yield (Baligar et al. 2001). Since NUE is a complex trait, the QTL mapping approach with a huge QTL and minimal overlap between studies is of limited use for improving NUE. Therefore, it is essential to undertake genetic dissection of NUE traits pertinent to the cropping region using suitable mapping panels or populations. Further, the precision can be further enhanced by the application of high-throughput phenotyping and modern biotechnological tools.

By utilizing the genetic variation for NUE-related traits, mapping approaches such as genome-wide association studies (GWAS) can be employed to dissect the QTL or genes associated with important NUE traits, particularly when merged with improved and precise phenotyping techniques (Poland et al. 2012; Cooper et al. 2014). The genomic regions and candidate genes identified through mapping approaches can be further analysed using forward and reverse genetics and transgenic approaches to improve crop yield (Wan et al. 2017). Further, genetic variation existing for agronomically important quantitative traits governed by small effect genes can be improved by novel breeding technique, i.e. genomic selection (GS), by predicting breeding values of individuals based on genome-wide marker data. The

implementation of novel breeding tools will fasten the rate of progress in genetic enhancement of NUE in major cereal crops, including rice, maize and polyploid with large and complex genomes such as wheat.

Different types of populations were used as association panels to carry out GWAS analysis. The existing varieties as a source of genetic variation have been utilized for association mapping approaches. The study of Monostori et al. (2017) used an elite germplasm set of 93 wheat varieties adapted to the Central European region. Significant phenotypic differences were observed for 15 investigated traits, including grain yield under low and normal N conditions. In another study, Rao et al. (2018) used 472 rice genotypes comprising landraces and breeding lines in a GWAS study and identified over a hundred genotypes with relative higher yield under low N conditions. In maize, association panel consisting of inbred lines and elite introgression lines was used for GWAS analysis for dissecting N and P use efficiency-related traits under low and optimum nutrient conditions (Xu et al. 2018; Ertiro et al. 2020; Wang et al. 2019b; Ma et al. 2020; Sun et al. 2020). Morosini et al. (2017) used an association panel comprising 64 inbred lines contrasting for N use efficiency and evaluated for N use efficiency-related traits such as total root length (TRL) and low nitrogen tolerance index (LNTI). These genetic resources possess different nutrient uptake and utilization mechanisms which are highly useful in developing nutrient use efficient varieties with higher grain yield. Further, well-characterized genotypes showing nutrient-responsive component traits and harbouring important candidate genes for NUE are valuable genetic resources for modern NUE breeding.

The analysis of QTLs with minor effects using traditional linkage mapping often present several limitations for complex polygenic traits like NUE owing to imprecise estimation and discrepancy in the detection of most of QTLs across mapping populations and target environments (Xu 2010). The advances in molecular breeding technologies helped breeders gain access to innovative genomic tools to gain high-density markers with genome-wide distribution. The genome-wide markers facilitate the genomic selection where genomic breeding values are estimated based on cumulative effects of all these markers' models. Genomic prediction affected by the size and genetic diversity of the training population and its relationship with the testing population (Pszczola et al. 2012). In rice, Liu et al. (2016) reported donor parent for plant height ratio of low N/normal N (PHR) and tiller number ratio of low N/normal N (TNR) through both the association analysis and genomic prediction approaches. Also, this study suggested that through genomic prediction, germplasms which have both high and low breeding values, respectively, can be selected by combining both PHR and TNR traits. The study of Fritsche-Neto et al. (2012) used 41 single-cross maize hybrids and observed higher genome-wide selection accuracy for root traits under low N and P stresses compared to phenotypic selection accuracy. Further, Lyra et al. (2017) used 49 maize inbred lines contrasting for N use efficiency to develop 738 single-cross hybrids and applied multi-trait genomic prediction for nitrogen response indices using different selection indices. The use of historical datasets generated from multi-environment trials in GS for N use efficiency helps to achieve wide adaptation. A recent study by Mastrodomenico et al. (2019) evaluated 552 maize hybrids under low (0 kg N ha^{-1}) and high N (252 kg N ha^{-1}) conditions

across 10 environments and observed best GS in the training population when both parents were present in the training and validation sets with larger training population size. Similarly, Ertiro et al. (2020) evaluated testcross hybrids of maize across 9 optimum and 13 managed low N-stressed sites and obtained moderate to high prediction accuracies for target traits under optimum and low N conditions. The above representative studies suggest that genomic selection for NUE-related traits in diverse cereal germplasm could benefit for NUE more than phenotypic selection and marker-assisted selection.

5.5 Different Genomic Approaches to Improve NUE in Major Cereals

Nitrogen, phosphorus and potassium (N, P, K) constitute the primary macronutrients required for optimum crop growth and yield. Plant ability to absorb and utilize nutrients largely depends on the genetic makeup and molecular and physiological mechanisms (Baligar et al. 2001). The in-depth knowledge on genetic basis of the molecular pathways underlying the nutrient use efficiency (NUE)-related traits is critical to optimize NUE and to improve crop yield. Genomic approaches such as genetic linkage mapping and quantitative trait locus (QTL) analysis are being performed to identify the loci governing the agronomically important traits, including NUE traits in crop plants (Ali et al. 2018; Hartley et al. 2020; Ranjan and Yadav 2019). The advent of decoded genomes and advances in genome sequencing technologies, along with the discovery of novel genome analysis computations, have led to the development of high-throughput, cost-effective single nucleotide polymorphisms (SNPs). SNP markers are widely employed for the construction of high-resolution genetic maps to dissect complex QTLs and the annotating function of underlying candidate genes of target traits (Alseekh et al. 2021). The GWAS provide for high-resolution mapping using a set of diverse genotypes and map-based cloning of complex trait genes. Genomic selection (GS) is another potential approach that uses markers covering the entire genome to predict genomic-estimated breeding values (GEBVs) of individuals. GS enhances the genetic gain and improves speed and efficiency of the breeding programmes (Spindel et al. 2015). A genome-assisted breeding approach for developing NUE efficient crop varieties is illustrated in Fig. 5.1. This section illustrates genomic approaches such as GWAS and GS that are being applied to genetically dissect various NUE traits in major cereal crops.

5.5.1 Genome-Wide Association Analysis

GWAS or linkage disequilibrium (LD) mapping is an approach for identifying the associations between traits and genetic markers in a large population (Mackay and Powell 2007). GWAS uses the diverse panel of genotypes (such as landraces, diverse germplasm, breeding populations, doubled haploid populations, etc.) to identify significant marker-trait associations (MTAs) with the power to identify multiple

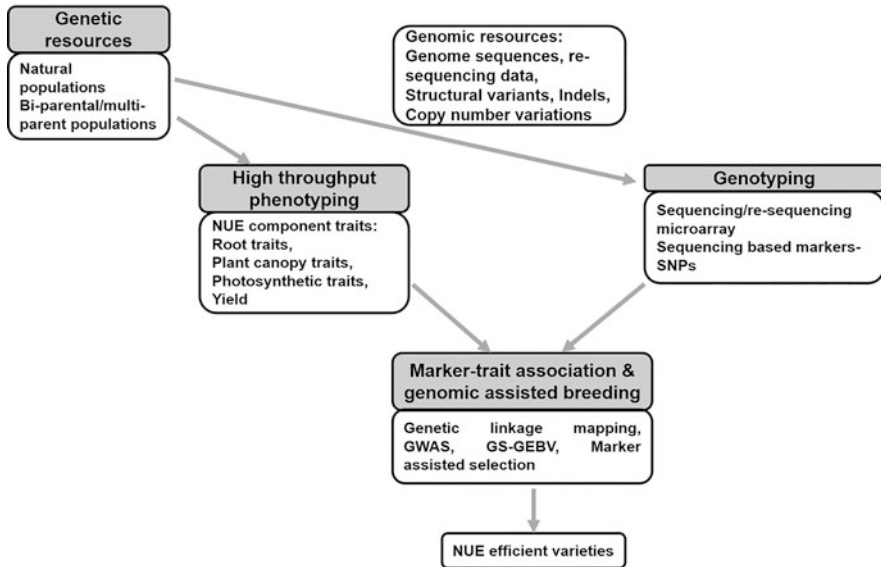


Fig. 5.1 Genome-assisted breeding approach for developing NUE efficient crop varieties: The genetic variation present in the crop germplasm pool can be identified using high-throughput phenotyping of NUE component traits for breeding higher NUE. The advances in genomic technologies in recent years have led to the development of large-scale genomic resources such as genome sequences and millions of genome-wide variations (such as SNPs, indels, SVs, CNVs). Using high-throughput genotyping and high-throughput precise phenotyping approaches, complex traits such as NUE component traits can be dissected at the genetic level by using genomic approaches such as QTL mapping, GWAS and whole genome prediction using genomic selection models and marker-assisted selection for developing NUE efficient crop varieties

loci with several alleles simultaneously (Wang et al. 2019b) and provides a very high genetic resolution based on historical as well as evolutionary recombination events (Chang et al. 2018). With the latest updates in NGS techniques coupled with computational tools, GWAS has become a potent technique for detecting the natural variations and QTLs governing the target phenotype. It has widely been used to understand the genetic basis of economically important complex traits in various crop plants including cereals (Zhao et al. 2011; Yang et al. 2014; Wang et al. 2017b; Liu and Yan 2018). Further, GWAS have been reported to delineate the nutrients' (N, P, K) use efficiency-related traits in different crop species, including major cereals such as rice, wheat and maize (Table 5.2).

5.5.2 Nitrogen Use Efficiency

Nitrogen is the most crucial nutrient element required for the growth of crop plants in natural ecosystems. Nitrogen use efficiency is reported to be a complex attribute governed by multiple genes (Yang et al. 2017), and its expression is regulated at

Table 5.2 List of association mapping studies related to nutrient use efficiency in major cereals

Crop	Association panel	Markers used	Environments	Year	Site	Treatments	Traits	QTL/MTA	Reference
<i>Nitrogen use efficiency</i>									
Rice	184 varieties	157 SSRs	1	1	1	Low and standard N	3	2	Liu et al. (2016)
	472 landraces and breeding lines	50 SSRs	1	2	1	LN=HN-100 kg N	9	12	Rao et al. (2018)
	461 accessions	1,531,224 SNPs	1	3	1	LN-0 N and HN-300 kg/ha N	6	7	Tang et al. (2019)
	190 japonica varieties	38,390 SNPs	1	2	1	LN and HN-120 kg N	16		Rakotoson et al. (2021)
Wheat	260 lines of core collection	3 TaGS2	1	1	1	LN and HN	5	34	Li et al. (2011)
	196 lines of core collection	899 (DArT, SSR, SNP)	12	2	3	LN=HN (35–120 kg N)	8	54	Bordes et al. (2013)
	214 commercial varieties	23,603 SNP	8	2	3	LN=HN-100 kg N	28	333	Cormier et al. (2014)
	93 cultivars	12,293 SNPs 13,160 silicoDArT markers	1	3	1	No N and N120 (120 kg N per ha)	16	183	Monostori et al. (2017)

Maize	64 inbred lines	616,201 SNPs	2	2	2	2	2	Low and ideal N	2	7	Morosini et al. (2017)
	411 inbred lines	955,120 SNPs	2	3	14	8	38—Optimum 45—Low	Low and optimum N	8		Ertiro et al. (2020)
	461 inbred lines	542,796 high-density SNPs	1	2	1	24	328	Low nitrate (LN, 0.05 mmol L ⁻¹) and high nitrate (HN, 5 mmol L ⁻¹)	24		Sun et al. (2020)
	226 doubled haploid lines	61,634 SNPs	1	1	1	24	84	HN (15 mmol L ⁻¹ NO ₃ ⁻) and LN (1.5 mmol L ⁻¹ NO ₃ ⁻)	24		Ma et al. (2020)
	139 inbred lines	50,790 SNPs	1	1	1	6	50	Normal N supply and low N supply	6		He et al. (2020)
<i>Phosphorus use efficiency</i>											
Rice	292 diverse accessions	44 K rice SNPs	2	2	2	9	6	Low P and a + P control	9		Wissuwa et al. (2015)
Wheat	82 diverse accessions	35 K SNP	2	2	1	15	78	Low (2.67 mg P kg ⁻¹ soil) and sufficient P (42.2 mg P kg ⁻¹ soil)	15		Soumya et al. (2021)
Maize	Panel a—410 inbred lines Panel B—475 inbred lines	55 K SNPs	2	2	2	11	264	NP and LP	11		Xu et al. (2018)
Maize	356 diverse inbred lines	56,110 SNPs	1	2	3	13	1157 SNPs across 1238 genes	P-deficient (nutrient solution without NH ₄ H ₂ PO ₄) and P-sufficient (complete nutrient solution containing 1 mmol L ⁻¹ NH ₄ H ₂ PO ₄)	13		Wang et al. (2019b)

(continued)

Table 5.2 (continued)

Crop	Association panel	Markers used	Environments	Year	Site	Treatments	Traits	QTL/MTA	Reference
<i>Potassium use efficiency</i>									
Rice	324 cultivars	SNPs	1	1	1	K + --deficient (0.1 mM) and K + --replete (1 mM) nutrient solutions	7	10 SNPs	Hartley et al. (2020)
Wheat	150 spring wheat varieties	90 K Infinium iSelect SNP array	1	3	1	Low K (0.09 g/kg of soil) and normal K (0.18 g/kg of soil)	18	534 mta 11 loci	Safdar et al. (2020)

different levels by transcription factors, allosteric regulation and post-transcriptional modification (Ranjan and Yadav 2019). Using bi-parental mapping populations, QTLs underlying NtUE have been identified in major cereals. Several researchers have located the genes encoding glutamate synthase (GS, GOGAT) or nitrate reductase (NR) in identified QTLs for N uptake and remobilization in different crop plants. In rice, Liu et al. (2016) used a population of 184 varieties and studied NUE traits (plant height, tiller number and grain length) in low and optimum N conditions. Association mapping, using genotyping data of 157 genome-wide simple sequence repeat (SSR) markers, identified 8 markers showing significant association with NUE traits. Of these, the genomic regions of two loci at RM5639 and RM3628 contained key NUE-related genes *GS1:2* and *AspAt3*, respectively. Grain yield is generally used as an indicator of NUE, and genotypes with higher NUE have the capacity to uptake N efficiently and divert it for grain yield production (Ali et al. 2018). A set of 472 landraces and breeding lines of rice were screened under low and recommended nitrogen (100 kg ha^{-1}) in field condition (Rao et al. 2018). The study revealed that traits such as grains on secondary branches, grain N concentration and yield are the likely target traits for selection. Further, GWAS analysis using a set of 50 SSR markers revealed about 12 genomic regions associated with yield and related traits under low nitrogen. Subsequent analysis of QTL regions detected three candidate genes (2-oxoglutarate/malate translocator, alanine aminotransferase and pyridoxal phosphate-dependent transferase) that showed enhanced expression in high-yielding genotypes under low N conditions. Tang et al. (2019) integrated GWAS with functional characterization of NtUE genes using a population consisting of rice landraces and identified an *OsNPF6.1^{HapB}*, a rare variant of nitrate transporter *OsNPF6.1* that enhances nitrogen use efficiency by increasing effective panicle number and yield per plant. Recently, Rakotoson et al. (2021) reported 369 significant SNPs belonging to 46 distinct haplotype groups associated with NtUE and yield-related component traits. Further, SNPs showing significant association with NtUE and yield traits co-localized with the genes are involved in N metabolism and transport. Also, the authors found that complex traits like grain yield and nitrogen use efficiency are governed by a several number of QTLs with minimal effects and such small effects can be captured through GWAS and genomic selection approaches.

In wheat, the function of the glutamine synthetase (GS) enzyme in controlling NtUE was proved through the correlation studies (Kichey et al. 2007). Further, haplotype studies of the genes encoding GS plastic isoforms and their association with N use and yield-associated traits revealed four favourable TaGS2 haplotypes (A1b, B1a, B1b, D1a) that may provide better growth, agronomic performance and N uptake for vegetative growth (Li et al. 2011). Previous studies had mapped QTLs related to N use and yield on the chromosomal location containing *GS2* in wheat (Yang et al. 2007; Laperche et al. 2007), indicating the importance of genomic regions surrounding *GS2* gene for breeding wheat cultivars with enhanced N use efficiency and yield. Further, Bordes et al. (2013) used an association panel of 196 accessions of a wheat core collection for GWAS analysis and identified 23 regions, spread over 16 chromosomes, for response to nitrogen level. Similarly,

Cormier et al. (2014) identified 333 genomic regions associated with 28 traits associated with NtUE in a panel of 214 European winter wheat varieties. These studies not only provided new insights on NUE genetic determinism but also assessed QTLs' co-localizations with known N uptake or assimilation enzymes. Recently, Monostori et al. (2017) used DArTseq markers in a GWAS study and identified 183 marker-trait associations (MTA) affecting N use-related complex agronomic traits. These significant genomic regions overlapped with the regions previously mapped for N uptake (Laperche et al. 2007; Xu et al. 2014) and N utilization efficiency (Guo et al. 2012) in wheat.

In maize, using 64 tropical maize inbred lines in a GWAS study, Morosini et al. (2017) showed 7 significant SNPs for low N tolerance index and total root length. Further, the candidate genes that were predicted within the mapped region were mostly engaged with transcriptional regulation and enzyme activity in the N cycle. Breeding maize for NUE is hampered by costly phenotypic screenings and trait complex nature of traits under low N. To circumvent this, Ertiro et al. (2020) identified 38 and 45 SNPs which showed significant association with grain yield (GY) and other traits under optimum and low N conditions, respectively, in a testcross progeny of 411 maize inbred lines. The significant SNPs were further analysed to predict 136 putative candidate genes. Sun et al. (2020) conducted GWAS and candidate gene mining for maize root traits under low N stress using a panel of 461 maize inbred lines. As a result, 328 significant SNPs associated with root and shoot traits were obtained. Upon mining of candidate genes, four genes within the 100-kb intervals flanking the SNPs were identified. Further, Ma et al. (2020) grew 226 DH population of maize under growth chamber with HN ($15 \text{ mmol L}^{-1} \text{ NO}_3^-$) or LN ($1.5 \text{ mmol L}^{-1} \text{ NO}_3^-$) and identified 51 and 33 SNPs, respectively, associated with RSA traits. Using these SNPs, candidate genes involved in seedling, seed and root system development or N metabolism were predicted. Recently, He et al. (2020) used a panel of 139 maize inbred lines to map 27 and 23 SNPs associated with complex NUE-related traits under normal and low N levels, respectively. Among the candidate genes identified, two genes, viz. *Zm00001d025831* and *Zm00001d004633*, encode ammonium transporter 1 and transmembrane amino acid transporter family protein, respectively.

5.5.2.1 Phosphorus Use Efficiency

Like any other nutrients, phosphorus use efficiency (PUE) has been described by two components, viz. P uptake and P utilization efficiency (Wang et al. 2010), and improving both components would be the appropriate approach for improved tolerance to P deficiency. In this direction, various studies have reported genes and QTLs controlling agronomic traits related to PUE in different crops (Bovill et al. 2013). However, relatively few studies have applied the GWAS approach to identify genes/QTLs for PUE in crop species. Wissuwa et al. (2015) characterized the genotypic variation for PUE using a rice panel comprising 292 diverse accessions by using a hydroponic system. GWAS analysis using 44 K rice SNPs identified several loci for PUE on chromosomes 1, 4, 11 and 12. Subsequent coding regions and expression analysis between genotypes of contrasting haplotypes revealed

functional changes in two predicted nucleic acid-interacting proteins that are likely causative factors for the observed haplotype-associated variations in PUE. In wheat, Soumya et al. (2021) phenotyped 82 bread wheat genotypes in soil and hydroponics at low and optimum P and performed GWAS analysis with 35 K SNPs. The study showed 78 marker-trait associations (MTAs) and 297 candidate genes involved in key biological processes. Maize is an important cereal showing enormous genetic variation and rapid LD decay, which is quite appropriate for GWAS. For low P stress tolerance, Xu et al. (2018) performed a GWAS using 2 natural populations of maize and identified 259 candidate genes that are associated with transcriptional regulation, scavenging of reactive oxygen species, hormone regulation and cell wall remodelling. Similarly, using 356 diverse inbred lines of maize, Wang et al. (2019b) obtained significant SNPs for 13 traits under P-sufficient and P-deficient conditions. Also, natural variations and haplotypes within the low stress-responsive genes associated with low P stress were detected for root traits. Further, different expression levels of candidate genes in response to low P stress identified candidate genes such as *GRMZM2G466545*, *GRMZM2G024530*, *GRMZM2G398848*, *GRMZM2G143204*, *GRMZM2G100652*, *GRMZM2G117250* and *GRMZM2G301738* that are previously reported by Zhang et al. (2014) under low P stress.

5.5.2.2 Potassium Use Efficiency

Potassium use efficiency (KUE) is a complex trait and combines of K uptake efficiency (KUpE) and K utilization efficiency (KUtE). Therefore, the genetic improvement of crops for KUE is carried out by identifying key genomic regions containing QTLs/genes associated with these traits. Despite this, a few QTL studies for KUE-related traits have been reported in major cereal crops using bi-parental mapping populations (Hartley et al. 2020; Ali et al. 2018; Safdar et al. 2020). With the availability of genome-wide SNP markers for the genotypes that represent the diverse background, the information on QTLs governing KUE using the GWAS approach is beginning to accumulate. In rice, a GWAS study with diverse genotypes identified ten SNPs for physiological responses to low potassium stress, including a sodium transporter gene *OsHKT2;1*, a key factor that impacts KUE (Hartley et al. 2020). In this study, the RGR-K signal identified on chromosome 1 overlapped with the QTL identified previously by Fang et al. (2015). Also, the tissue sodium-associated signals found on chromosome 6 related to Na⁺ uptake in this study were earlier described by Miyamoto et al. (2012). Similarly, in wheat, the study by Safdar et al. (2020) used a panel of 150 spring wheat varieties to identify 534 significant associations. Further analysis of these marker-trait associations led to the detection of 11 stable loci that are associated with potassium use efficiency and other important agronomic traits.

5.5.3 Genomic Selection

Most agriculturally important traits, including NUE-related traits, are reported to be polygenic in nature and governed by many genes with minor effects accounting for a small proportion of total genetic variances (Robertson et al. 2019). These small effect genes/QTLs are difficult to map and use simultaneously in the breeding through traditional linkage and QTL mapping (Lande and Thompson 1990). As a consequence, marker-assisted selection (MAS) has a limited success in improving such traits (Heffner et al. 2009). Genomic selection (GS) is a potential tool that overcomes the limitations of MAS for quantitative traits. GS uses genome-wide markers to predict the individual's genetic potential instead of identifying the specific QTL. Advances in NGS technologies, including the availability of high-throughput, cost-effective, informative SNP arrays and improved statistical methods to accurately predict marker effects, have led to the application of GS in making selection decisions in crop plants. GS greatly improves the accuracy of selection, speed and efficiency of breeding programmes. GS has been widely applied to enhance grain yield and other agronomical traits in major crop plants (Robertson et al. 2019; Srivastava et al. 2020).

Liu et al. (2016) in rice explored the potential of marker-based prediction as a novel approach for NtUE breeding. For this, they used 157 genome-wide SSR marker data for GS by ridge regression and best linear unbiased prediction mixed models (RR-BLUP) to assess the genomic prediction accuracy for plant height ratio and tiller number ratio under normal and low N conditions and found high prediction accuracies for plant height ratio. Root traits are crucial for the uptake of nutrients in maize. Fritsche-Neto et al. (2012) assessed the accurateness of the genome-wide selection (GWS) in maize for root traits under N and P stress using 41 single-cross hybrids. It was showed that, based on hybrid data, the genomic prediction Scheme (RR-BLUP) generated higher GWS accuracy than the phenotypic selection for all the traits. Evaluation and comparison of prediction accuracies by single- and multi-trait models were performed in 738 maize single-cross hybrids derived from 49 tropical inbred lines contrasting for N regimes. The study reported the suitability of multi-trait genomic prediction with a combination of different selection indices and showed the advantage of using single-trait RKHS and GK multi-trait than GBLUP (Lyra et al. 2017). Similarly, evaluation of 552 maize hybrids under low (0 kg N ha^{-1}) and optimum N (252 kg N ha^{-1}) situations across 10 environments showed improved prediction accuracies in larger training and test population when parental lines are included. However, the prediction accuracy on response to training population size and composition was found to be dependent on the N use trait (Mastrodomenico et al. 2019). Additionally, moderate to high prediction accuracies for grain yield and other traits under low N conditions were reported in maize (Ertiro et al. 2020). For low phosphorus stress tolerance in maize, Xu et al. (2018) validated 5 classical genomic selection models for 11 traits under low P ($0 \text{ kg/ha P}_2\text{O}_5$) and normal P ($120 \text{ kg/ha P}_2\text{O}_5$) conditions and found that traits with higher heritability had higher prediction accuracy and, with respect to marker density, a moderate density of SNP markers (8000 SNPs) would be appropriate to achieve precise predictions on low

phosphorus tolerance traits. Several of these studies used GWAS in conjunction with GS and found that integrating the powerful GWAS results increased prediction accuracy of GS and will improve breeding efficiency for higher nutrient use efficiency.

5.6 Prospects and Conclusion

N, P and K are the vital macronutrients required for plant growth and development, including crop yield and quality. Injudicious use of inorganic fertilizers to meet the nutrient demand of crop plants for achieving higher crop yields is a major cause of environmental pollution and financial burden to the farmers. In light of scarce resources and increased cost of fertilizer production, the development of cultivars with higher nutrient use efficiency is the most feasible approach for sustainable crop growth and yield, especially under low nutrient soils (Baligar et al. 2001; Sarkar and Baishya 2017). To genetically improve nutrient uptake and utilization efficiency in crop plants, we need to understand the molecular genetic mechanisms underlying nutrient use efficiency in crops. Breeding for improved NUE relies on the identification of genetic variation in component traits within germplasm lines, high-throughput precise phenotyping of NUE-related traits in large number of germplasm lines, molecular tagging of NUE phenotypes and finally introgressing beneficial traits into elite cultivars or locally adapted germplasm (White 2013; White and Bell 2017). A large useful genetic variation for component traits related to N, P and K use efficiency has been reported in major cereals (rice, wheat, maize), which provides an opportunity to exploit diverse germplasm lines to identify efficiency alleles and breed for genotypes with higher NUE (White 2013). Such genetic material needs to be screened for NUE parameters using appropriate phenotyping techniques targeting canopy, photosynthetic traits using optical sensors (Erdle et al. 2011) and crop indices such as NDVI (normalized difference vegetation index) (Aparicio et al. 2000) to measure canopy development and canopy nutritional status with both ground-based and aerial imagery devices (Knyazikhin et al. 2013; Li et al. 2013). In addition, efficient uptake of nutrients by root systems is critical to improve the NUE in cereal crops; hence, there is a scope for genetic improvement of root traits.

At the molecular level, plant NPK use efficiency is highly complex involving the integration of many genes and regulatory elements for nutrient sensing, uptake, translocation, assimilation and remobilization which are under the strong influence of environmental variation (Yang et al. 2017; Wang et al. 2014; Gong et al. 2015). Therefore, identification of large-effect QTLs/genes and molecular regulators is challenging. Despite this, many researchers attempted to map complex NPK use efficiency and component traits in major cereals (rice, wheat, maize) with varying degrees of phenotypic variation using molecular markers and advanced biotechnological tools. Combined genomic and phenomic studies so far identified several QTLs and genes for NPK acquisition and transportation in variable genetic backgrounds under diverse doses of NPK. In recent years, better statistical tools for genetic mapping have been developed, and it has been recognized the necessity

for more careful experimental design and replicate testing (Myles et al. 2009; Tong et al. 2014). Further, recent innovations in molecular marker tools and sequencing chemistries have led to the development of a cost-effective integrative SNP array for diverse breeding applications, including GWAS and GS. Several studies used the GWAS approach by integrating ‘omics’ data and identified a number of markers associated with NUE-related traits and key loci/genes governing plant yield along with NPK uptake and utilization in major cereals. However, functional validation of NUE-associated structural or regulatory genes was rarely successful. With the availability of genome-wide SNP markers and powerful computational methods to accurately predict marker effects, novel breeding approaches such as genomic selection (GS) with whole genome prediction models have become convincing strategy to select even for minor QTLs and accelerate the genetic gain. All these efforts require a collective holistic strategy integrating with novel omics tools for the effective implementation of NUE breeding programmes for developing well-adapted and more nutrient-efficient cultivars.

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References

- Agrama HAS, Zakaria AG, Said FB, Tuinstra M (1999) Identification of quantitative trait loci for nitrogen use efficiency in maize. *Mol Breed* 5:187–195. <https://doi.org/10.1023/A:1009669507144>
- Ahmed M, Saeed NA, Ashraf YM, Mukhtar Z, Mansoor S (2020) Improving nitrogen use efficiency in wheat (*Triticum aestivum* L.) through transformation of codon optimized *alanine aminotransferase* gene. *Pak J Agri Sci* 57(3):707–714. <https://doi.org/10.21162/PAKJAS/20.9032>
- Ali J, Jewel ZA, Mahender A, Anandan A, Hernandez J, Li Z (2018) Molecular genetics and breeding for nutrient use efficiency in rice. *Int J Mol Sci* 19(6):1762. <https://doi.org/10.3390/ijms19061762>
- Alseekh S, Kostova D, Bulut M et al (2021) Genome-wide association studies: assessing trait characteristics in model and crop plants. *Cell Mol Life Sci* 78:5743–5754. <https://doi.org/10.1007/s00018-021-03868-w>
- Andresen M, Dresbøll DB, Stoumann Jensen L, Magid J, Thorup-Kristensen K (2016) Cultivar differences in spatial root distribution during early growth in soil, and its relation to nutrient uptake—a study of wheat, onion and lettuce. *Plant Soil* 408:255–270. <https://doi.org/10.1007/s11104-016-2932-z>
- Aparicio N, Villegas D, Casadesus J, Araus JL, Royo C (2000) Spectral vegetation indices as non-destructive tools for determining durum wheat yield. *Agron J* 92:83–91. <https://doi.org/10.2134/agronj2000.92183x>
- Araki R, Hasegawa H (2006) Expression of rice (*Oryza sativa* L.) genes involved in high-affinity nitrate transport during the period of nitrate induction. *Breed Sci* 56:295–302. <https://doi.org/10.1270/jsbbs.56.295>

- Ashley K, Cordell D, Mavinic D (2011) A brief history of phosphorus: from the philosopher's stone to nutrient recovery and reuse. *Chemosphere* 84(6):737–746. <https://doi.org/10.1016/j.chemosphere.2011.03.001>
- Atiq M, Javed N, Urooj S, Bukhari A, Ali Y, Zeeshan A, Jabbar A (2017) Management of leaf rust of wheat through different levels of NPK and sowing times. *Ad Zool Bot* 5:39–44. <https://doi.org/10.13189/azb.2017.050401>
- Baligar VC, Fageria NK, Hea ZL (2001) Nutrient use efficiency in plants. *Commun Soil Sci Plant Anal* 32:7–8. <https://doi.org/10.1081/CSS-100104098>
- Barber SA, Cushman JH (1981) Nitrogen uptake model for agronomic crops. In: Iskander IK (ed) *Modeling wastewater renovation-land treatment*. Wiley-Interscience, New York, pp 382–409
- Barber SA, Silverbush M (1984) Plant root morphology and nutrient uptake. In: Barber SA, Bouldin DR, Kral DM, Hawkins SL (eds) *Roots, nutrient and water influx and plant growth*, ASA special publication number, vol 49. American Society of Agronomy, Madison, WI, pp 65–88
- Batjes NH (1997) A world data set of derived soil properties by FAO UNESCO soil unit for global modelling. *Soil Use Manag* 13:9–16. <https://doi.org/10.1111/j.1475-2743.1997.tb00550.x>
- Beaton JD, Sekhon GS (1985) Potassium nutrition of wheat and other small grains. In: Munson RD (ed) *Potassium in agriculture*. ASA, CSSA and SSSA, Madison, WI, pp 701–752
- Berzsenyi Z, Györfy B, Lap D (2000) Effect of crop rotation and fertilisation on maize and wheat yields and yield stability in a long-term experiment. *Eur J Agron* 13(2–3):225–244. [https://doi.org/10.1016/S1161-0301\(00\)00076-9](https://doi.org/10.1016/S1161-0301(00)00076-9)
- Bordes J, Ravel C, Jaubertie JP, Duperrier B, Gardet O et al (2013) Genomic regions associated with the nitrogen limitation response revealed in a global wheat core collection. *Theor Appl Genet* 126:805–822. <https://doi.org/10.1007/s00122-012-2019-z>
- Bovill WD, Huang CY, McDonald GK (2013) Genetic approaches to enhancing phosphorus-use efficiency (PUE) in crops: challenges and directions. *Crop Pasture Sci* 64:179–198. <https://doi.org/10.1071/CP13135>
- Brar MS, Bijay-Singh BSK, Srinivasarao C (2011) Role of potassium nutrition in nitrogen use efficiency in cereals. *Res Find e-ific* 29:20–27
- Bruen ETLV, Struik PC (2017) Diverse concept of breeding for nitrogen use efficiency. A review. *Agron Sustain Dev* 37:50. <https://doi.org/10.1007/s13593-017-0457-3>
- Cai C, Wang JY, Zhu YG, Shen QR, Li B, Tong YP, Li ZS (2008) Gene structure and expression of the high-affinity nitrate transport system in rice roots. *J Integr Plant Biol* 50:443–451. <https://doi.org/10.1111/j.1744-7909.2008.00642.x>
- Chang F, Guo C, Sun F, Zhang J, Wang Z, Kong J et al (2018) Genome-wide association studies for dynamic plant height and number of nodes on the main stem in summer sowing soybeans. *Front Plant Sci* 9:1184. <https://doi.org/10.3389/fpls.2018.01184>
- Chankaew S, Monkham T, Pinta W, Sanitchon J, Kaewpradit W, Srinives P (2019) Screening tolerance to phosphorus deficiency and validation of phosphorus uptake 1 (Pup1) gene-linked markers in Thai indigenous upland Rice germplasm. *Agronomy* 9(2):81. <https://doi.org/10.3390/agronomy9020081>
- Ciampitti IA, Murrell ST, Camberato JJ, Tuinstra M, Xia Y, Friedemann P, Vyn TJ (2013) Physiological dynamics of maize nitrogen uptake and partitioning in response to plant density and nitrogen stress factors: II. Reproductive phase. *Crop Sci* 53:2588–2602. <https://doi.org/10.2135/cropsci2013.01.0041>
- Ciampitti IA, Vyn TJ (2011) A comprehensive study of plant density consequences on nitrogen uptake dynamics of maize plants from vegetative to reproductive stages. *Field Crops Res* 121:2–18. <https://doi.org/10.1016/j.fcr.2010.10.009>
- Ciampitti IA, Vyn TJ (2012) Physiological perspectives of changes over time in maize yield dependency on nitrogen uptake and associated nitrogen efficiencies: a review. *Field Crops Res* 133:48–67. <https://doi.org/10.1016/j.fcr.2012.03.008>

- Cooper M, Messina CD, Podlich D, Totir LR, Baumgarten A, Hausmann NJ, Wright D, Graham G (2014) Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction. *Crop Pasture Sci* 65(4):311–336. <https://doi.org/10.1071/CP14007>
- Cordell D, Drangert JO, White S (2009) The story of phosphorus: global food security and food for thought. *Glob Environ Chang* 19(2):292–305. <https://doi.org/10.1016/j.gloenvcha.2008.10.009>
- Cormier F, Gouis JL, Dubreuil P, Lafarge S, Praud S (2014) A genome-wide identification of chromosomal regions determining nitrogen use efficiency components in wheat (*Triticum aestivum* L.). *Theor Appl Genet* 127:2679–2693. <https://doi.org/10.1007/s00122-014-2407-7>
- Curci PL, Cigliano RA, Zuluaga DL, Janni M, Sanseverino W, Sonnante G (2017) Transcriptomic response of durum wheat to nitrogen starvation. *Sci Rep* 7:1176. <https://doi.org/10.1038/s41598-017-01377-0>
- Dogan R, Bilgili U (2010) Effects of previous crop and N-fertilization on seed yield of winter wheat (*Triticum aestivum* L.) under rain-fed Mediterranean conditions. *Bulgarian J Agric Sci* 16:733–739
- Duncan EG, O'Sullivan CA, Roper MM, Palta J, Whisson K, Peoples MB (2018) Yield and nitrogen use efficiency of wheat increased with root length and biomass due to nitrogen, phosphorus, and potassium interactions. *J Plant Nutr Soil Sci* 181(3):364–373. <https://doi.org/10.1002/jpln.201700376>
- Ebelhar SA, Varsa EC (2000) Tillage and potassium placement effects on potassium utilization by corn and soybean. *Commun Soil Sci Plant Anal* 31:11–14. <https://doi.org/10.1080/00103620009370591>
- Eghball B, Maranville JW (1993) Root development and nitrogen influx of corn genotypes grown under combined water and nitrogen stresses. *Agron J* 85:147–152. <https://doi.org/10.2134/agronj1993.00021962008500010027x>
- Ehdaie B, Merhaut DJ, Ahmadian S, Hoops AC, Khuong T, Layne AP, Waines JG (2010) Root system size influences water-nutrient uptake and nitrate leaching potential in wheat. *J Agron Crop Sci* 196:455–466. <https://doi.org/10.1111/j.1439-037X.2010.00433.x>
- Erdle K, Mistele B, Schmidhalter U (2011) Comparison of active and passive spectral sensors in discriminating biomass parameters and nitrogen status in wheat cultivars. *Field Crops Res* 124(1):74–84. <https://doi.org/10.1016/j.fcr.2011.06.007>
- Ertiro BT, Labuschagne M, Olsen M, Das B, Prasanna BM, Gowda M (2020) Genetic dissection of nitrogen use efficiency in tropical maize through genome-wide association and genomic prediction. *Front Plant Sci* 11:474. <https://doi.org/10.3389/fpls.2020.00474>
- Fang Y, Wu W, Zhang X, Jiang H, Lu W, Pan J, Hu J, Guo L, Zeng D, Xue D (2015) Identification of quantitative trait loci associated with tolerance to low potassium and related ions concentrations at seedling stage in rice (*Oryza sativa* L.). *Plant Growth Regul* 77:157–166. <https://doi.org/10.1007/s10725-015-0047-9>
- Fang Z, Xia K, Yang X, Grotemeyer MS, Meier S, Rentsch D, Xu X, Zhang M (2013) Altered expression of the PTR/NRT1 homologue OsPTR9 affects nitrogen utilization efficiency, growth and grain yield in rice. *Plant Biotechnol J* 11:446–458. <https://doi.org/10.1111/pbi.12031>
- FAO (2016) World fertilizer trends and outlook to 2019. Food and Agriculture Organization of the United Nations, Rome. <http://www.fao.org/3/a-i5627e.pdf>
- Feng H, Yan M, Fan X, Li B, Shen Q, Miller AJ, Xu G (2011) Spatial expression and regulation of rice high-affinity nitrate transporters by nitrogen and carbon status. *J Exp Bot* 62:2319–2332. <https://doi.org/10.1093/jxb/erq403>
- Fritsche-Neto R, DoVale JC, Lanes ECM, Resende MDV, Miranda GV (2012) Genome-wide selection for tropical maize root traits under conditions of nitrogen and phosphorus stress. *Acta Scientiarum* 34(4):389–395. <https://doi.org/10.4025/actasciagron.v34i4.15884>
- Gallais A, Coque M (2005) Genetic variation and selection for nitrogen use efficiency in maize: a synthesis. *Maydica* 50:531–547
- Garnett T, Plett D, Heuer S, Okamoto M (2015) Genetic approaches to enhancing nitrogen-use efficiency (NUE) in cereals: challenges and future directions. *Funct Plant Biol* 42:921–941. <https://doi.org/10.1071/FP15025>

- Gattward JN, Almeida AA, Souza JO Jr, Gomes FP, Kronzucker HJ (2012) Sodium-potassium synergism in *Theobroma cacao*: stimulation of photosynthesis, water-use efficiency and mineral nutrition. *Physiol Plant* 146:350–362. <https://doi.org/10.1111/j.1399-3054.2012.01621.x>
- Gauer LE, Grant CA, Gehl DT, Bailey LD (1992) Effects of nitrogen fertilization on grain protein content, nitrogen uptake, and nitrogen use efficiency of six spring wheat (*Triticum aestivum* L.) cultivars, in relation to estimated moisture supply. *Can J Plant Sci* 72:235–241. <https://doi.org/10.4141/cjps92-026>
- Geiger HH (2009) Agronomic traits and maize modifications: nitrogen use efficiency. In: Bennetzen JL, Hake SC (eds) *Handbook of maize: its biology*. Springer Science, New York, pp 405–417
- Giles CD, Brown LK, Adu MO, Mezeli MM, Sandral GA, Simpson RJ, Wendler R, Shand CA, Menezes-Blackburn D, Darch T, Stutter MI, Lumsdon DG, Zhang H, Blackwell MSA, Wearing C, Cooper P, Haygarth PM, George TS (2017) Response-based selection of barley cultivars and legume species for complementarity: root morphology and exudation in relation to nutrient source. *Plant Sci* 255:12–28. <https://doi.org/10.1016/j.plantsci.2016.11.002>
- Gill HS, Anoop S, Sethi SK, Behl RK (2004) Phosphorous uptake and use efficiency in different varieties of bread wheat (*Triticum aestivum* L.). *Arch Agron Soil Sci* 50:563–572. <https://doi.org/10.1080/03650340410001729708>
- Gong X-P, Liang X, Guo Y, Wu C-H, Zhao Y, Li X-H, Li S-S, Kong F-M (2015) Quantitative trait locus mapping for potassium use efficiency traits at the seedling stage in wheat under different nitrogen and phosphorus treatments. *Crop Sci* 55:2690–2700. <https://doi.org/10.2135/cropsci2014.10.0711>
- Gulser C, Zharlygasov Z, Kızılkaya R, Kalimov N, Akca I, Zharlygasov Z (2019) The effect of NPK foliar fertilization on yield and macronutrient content of grain in wheat under Kostanai-Kazakhstan conditions. *Eurasian J Soil Sci* 8:275–281. <https://doi.org/10.18393/ejss.575026>
- Guo Y, Kong FM, Feng XY, Zhao Y, Liang X, Wang Y (2012) QTL mapping for seedling traits in wheat grown under varying concentrations of N, P and K nutrients. *Theor Appl Genet* 124:851–865. <https://doi.org/10.1007/s00122-011-1749-7>
- Guttieri MJ, Frels K, Regassa T, Waters BM, Baenziger PS (2017) Variation for nitrogen use efficiency traits in current and historical great plains hard winter wheat. *Euphytica* 213:87. <https://doi.org/10.1007/s10681-017-1869-5>
- Haeder HE, Beringer H (1981) Influence of potassium nutrition and water stress on the content of abscisic acid in grains and flag leaves of wheat during grain-development. *J Sci Food Agric* 32: 552–556. <https://doi.org/10.1002/jfsa.2740320605>
- Haileelassie B, Habte D, Haileelassie M, Gebremeskel G (2014) Effects of mineral nitrogen and phosphorus fertilizers on yield and nutrient utilization of bread wheat (*Triticum aestivum*) on the sandy soils of Hawzen District, northern Ethiopia. *Agric Fish* 3:189–198. <https://doi.org/10.11648/j.aff.20140303.18>
- Hari-Gowthem G, Kaur S, Sekhon BS, Sharma P, Chhuneja P (2019) Genetic variation for phosphorus-use efficiency in diverse wheat germplasm. *J Crop Improv* 33(4):536–550. <https://doi.org/10.1080/15427528.2019.1627633>
- Hartley TN, Thomas AS, Maathuis FJM (2020) A role for the OsHKT 2;1 sodium transporter in potassium use efficiency in rice. *J Exp Bot* 71(2):699–706. <https://doi.org/10.1093/jxb/erz113>
- Hastings DF, Gutknecht J (1978) Potassium and turgor pressure in plants. *J Theor Biol* 73:363–366. [https://doi.org/10.1016/0022-5193\(78\)90197-2](https://doi.org/10.1016/0022-5193(78)90197-2)
- He K, Xu S, Zhang X, Li Y, Chang L, Wang Y, Shi Y, Cui T, Dong Y, Lan T, Liu X, Du Y, Zhang R, Liu J, Xue J (2020) Mining of candidate genes for nitrogen use efficiency in maize based on genome-wide association study. *Mol Breed* 40:83. <https://doi.org/10.1007/s11032-020-01163-3>
- Heffner EL, Sorrells ME, Jannink JL (2009) Genomic selection for crop improvement. *Crop Sci* 49: 1–12. <https://doi.org/10.2135/cropsci2008.08.0512>

- Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237:173–195. <https://doi.org/10.1023/A:1013351617532>
- Hirel B, Berlin P, Quillere I, Bourdoncle W, Attagnant C, Dellay C, Gouy A, Cadiou S, Retailiau C, Falque M, Gallais A (2001) Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. *Plant Physiol* 125:1258–1270. <https://doi.org/10.1104/pp.125.3.1258>
- Hirel B, Le Gouis J, Ney B, Gallais A (2007) The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. *J Exp Bot* 58(9):2369–2387. <https://doi.org/10.1093/jxb/erm097>
- Hu B, Wang W, Ou S, Tang J, Li H, Che R, Zhang Z, Chai X, Wang H, Wang Y, Liang C, Liu L, Piao Z, Deng Q, Deng K, Xu C, Liang Y, Zhang L, Li L, Chu C (2015) Variation in *NRT1.1B* contributes to nitrate-use divergence between rice subspecies. *Nat Genet* 47(7):834–838. <https://doi.org/10.1038/ng.3337>
- Hussain N, Khan MB, Ahmad R (2008) Influence of phosphorus application and sowing time on performance of wheat in calcareous soils. *Int J Agric Biol* 10:399–404
- Hussain MI, Shah SH, Hussain S, Iqbal K (2002) Growth, yield and quality response of three wheat (*Triticum aestivum* L.) varieties to different levels of N, P and K. *Int J Agric Biol* 4:362–364
- Jan MF, Khan AA, Liaqat W, Ahmad H, Rehan W (2018) Phenology, growth, yield and yield components of maize (*Zea mays* L.) hybrids to different levels of mineral potassium under semiarid climate. *Agri Res Tech* 15:0027–0031. <https://doi.org/10.19080/ARTOAJ.2018.15.555943>
- Jeong K, Julia CC, Waters DLE, Pantoja O, Wissuwa M, Heuer S, Liu L, Rose TJ (2017) Remobilisation of phosphorus fractions in rice flag leaves during grain filling: implications for photosynthesis and grain yields. *PLoS One* 12(11):e0187521. <https://doi.org/10.1371/journal.pone.0187521>
- Jia C, Wang F, Yuan J, Zhang Y, Zhao Z, Abulizi B et al (2020) Screening and comprehensive evaluation of rice (*Oryza sativa* L. subsp. japonica Kato) germplasm resources for nitrogen efficiency in Xinjiang, China. *Plant Gen Resources* 18(3):179–189. <https://doi.org/10.1017/S1479262120000118>
- Jia Y, Yang X, Feng Y, Jilani G (2008) Differential response of root morphology to potassium deficient stress among rice genotypes varying in potassium efficiency. *J Zhejiang Univ Sci* 9: 427–434. <https://doi.org/10.1631/jzus.B0710636>
- Kichey T, Hirel B, Heumez E, Dubois F, Le Gouis J (2007) In winter wheat (*Triticum aestivum* L.), post-anthesis nitrogen uptake and remobilisation to the grain correlates with agronomic traits and nitrogen physiological markers. *Field Crop Res* 102:22–32. <https://doi.org/10.1016/j.fcr.2007.01.002>
- Knyazikhin Y, Schull MA, Stenberg P, Mottus M, Rautiainen M, Yang Y, Marshak A, Carmona PL, Kaufmann RK, Lewis P et al (2013) Hyperspectral remote sensing of foliar nitrogen content. *Proc Natl Acad Sci U S A* 110:E185–E192. <https://doi.org/10.1073/pnas.1210196109>
- Krafczyk I, Trollenier G, Beringer H (1984) Soluble root exudates of maize: influence of potassium supply and rhizosphere microorganisms. *Soil Biol Biochem* 16:315–322. [https://doi.org/10.1016/0038-0717\(84\)90025-7](https://doi.org/10.1016/0038-0717(84)90025-7)
- Lambers H, Cawthray GR, Giavalisco P, Kuo J, Laliberté E, Pearse SJ, Scheible WR, Stitt M, Teste F, Turner BL (2012) Proteaceae from severely phosphorus-impooverished soils extensively replace phospholipids with galactolipids and sulfolipids during leaf development to achieve a high photosynthetic phosphorus-use-efficiency. *New Phytol* 196:1098–1108. <https://doi.org/10.1111/j.1469-8137.2012.04285.x>
- Lammerts van Bueren ET, Struik PC (2017) Diverse concepts of breeding for nitrogen use efficiency: a review. *Agron Sustain Dev* 37:50. <https://doi.org/10.1007/s13593-017-0457-3>
- Lande R, Thompson R (1990) Efficiency of marker-assisted selection in the improvement of quantitative traits. *Genetics* 124:743–756. <https://doi.org/10.1093/genetics/124.3.743>

- Laperche A, Brancourt-Hulmel M, Heumez E, Gardet O, Hanocq E, Devienne-Barret F, Le Gouis J (2007) Using genotype \times nitrogen interaction variables to evaluate the QTL involved in wheat tolerance to nitrogen constraints. *Theor Appl Genet* 115:399–415. <https://doi.org/10.1007/s00122-007-0575-4>
- Leghari A, Laghari GM, Ansari MA, Mirjat MA, Laghari UA, Leghari SJ, Laghari AH, Abbasi ZA (2016) Effect of NPK and boron on growth and yield of wheat variety TJ-83 at Tandojam soil. *Adv Environ Biol* 10:209–216
- Li X, Mang M, Piepho HP, Melchinger A, Ludewig U (2021) Decline of seedling phosphorous use efficiency in the heterotic pool of flint maize breeding lines since the onset of hybrid breeding. *J Agro Crop Sci* 207:857–872. <https://doi.org/10.1111/jac.12514>
- Li XP, Zhao XQ, He X, Zhao GY, Li B, Liu DC, Zhang AM, Zhang XY, Tong YP, Li ZS (2011) Haplotype analysis of the genes encoding glutamine synthetase plastic isoforms and their association with nitrogen-use- and yield-related traits in bread wheat. *New Phytol* 189(2): 449–458. <https://doi.org/10.1111/j.1469-8137.2010.03490.x>
- Li HL, Zhao CJ, Huang WJ, Yang GJ (2013) Non-uniform vertical nitrogen distribution within plant canopy and its estimation by remote sensing: a review. *Field Crops Res* 142:75–84. <https://doi.org/10.1016/j.fcr.2012.11.017>
- Lindsay WL, Vlek PLG, Chien SH (1989) Phosphate minerals. In: Dixon JB, Weed SB (eds) *Minerals in soil environments*, 2nd edn. Soil Science Society of America, Madison, WI, pp 1089–1130
- Liu D, Shi Y (2013) Effects of different nitrogen fertilizer on quality and yield in winter wheat. *Adv J Food Sci Technol* 5(5):646–649. <https://doi.org/10.19026/ajfst.5.3141>
- Liu HJ, Yan JB (2018) Crop genome-wide association study: a harvest of biological relevance. *Plant J* 97:8–18. <https://doi.org/10.1111/tbj.14139>
- Liu ZY, Zhu CS, Jiang Y, Tian YL, Yu J, An HZ, Tang WJ, Sun J, Tang JP, Chen GM, Zhai HQ, Wang CM, Wan JM (2016) Association mapping and genetic dissection of nitrogen use efficiency-related traits in rice (*Oryza sativa* L.). *Funct Integr Genomics* 16:323–333. <https://doi.org/10.1007/s10142-016-0486-z>
- Lynch JP (2007) Roots of the second green revolution. *Aust J Bot* 55:1–20. <https://doi.org/10.1071/BT06118>
- Lyra DH, de Freitas ML, Galli G, Alves FC et al (2017) Multi-trait genomic prediction for nitrogen response indices in tropical maize hybrids. *Mol Breed* 37:80. <https://doi.org/10.1007/s11032-017-0681-1>
- Ma L, Qing C, Frei U, Shen Y, Lübberstedt T (2020) Association mapping for root system architecture traits under two nitrogen conditions in germplasm enhancement of maize doubled haploid lines. *Crop J* 8(2):213–226. <https://doi.org/10.1016/j.cj.2019.11.004>
- Mackay I, Powell W (2007) Methods for linkage disequilibrium mapping in crops. *Trends Plant Sci* 12:57–63. <https://doi.org/10.1016/j.tplants.2006.12.001>
- Maharajan T, Roch GV, Ceasar SA (2021) Recent advancements of molecular breeding and functional genomics for improving nitrogen-, phosphorus-, and potassium-use efficiencies in wheat. *Molecular breeding in wheat, maize and sorghum: Strategies for improving abiotic stress tolerance and yield*. pp: 170–96. doi: <https://doi.org/10.1079/9781789245431.0009>
- Maranville JW, Clark RB, Ross WW (1980) Nitrogen efficiency in grain sorghum. *J Plant Nutr* 2: 577–589. <https://doi.org/10.1080/01904168009362800>
- Maranville JW, Madhavan S (2002) Physiological adaptations for nitrogen use efficiency in sorghum. *Plant Soil* 245:25–34
- Marchi G, Silva VA, Guilherme LRG, Lima JM, Nogueira FD, Guimaraes PTG (2012) Potassium extractability from soils of Brazilian coffee regions. *Biosci J* 28:913–919
- Marschner H, Römheld V, Horst WJ, Martin P (1986) Root-induced changes in the rhizosphere: importance for the mineral nutrition of plants. *J Plant Nutr Soil Sci* 149(4):441–456. <https://doi.org/10.1002/jpln.19861490408>
- Martin A, Lee J, Kichey T, Gerentes D, Zivy M, Tatout C, Dubois F, Balliau T, Valot B, Davanture M, Terc'e-Laforgue T, Quiller'e I, Coque M, Gallais A, Gonzalez-Moro M-B,

- Bethencourt L, Habash DZ, Lea PJ, Charcosset A, Perez P, Murigneux A, Sakakibara H, Edwards KL, Hirel B (2006) Two cytosolic glutamine synthetase isoforms of maize are specifically involved in the control of grain production. *Plant Cell* 18:3252–3274. <https://doi.org/10.1105/tpc.106.042689>
- Masclaux-Daubresse C, Daniel-Vedele F, Dechorgnat J, Chardon F, Gaufichon L, Suzuki A (2010) Nitrogen uptake, assimilation and remobilization in plants: challenges for sustainable and productive agriculture. *Ann Bot* 105:1141–1157. <https://doi.org/10.1093/aob/mcq028>
- Mastrodomenico AT, Bohn MO, Lipka AE, Below FE (2019) Genomic selection using maize ex-plant variety protection germplasm for the prediction of nitrogen-use traits. *Crop Sci* 59:212–220. <https://doi.org/10.2135/cropsci2018.06.0398>
- McDonald G, Bovill W, Huang C, Lightfoot D (2013) Nutrient use efficiency. In: Kole C (ed) *Genomics and breeding for climate-resilient crops*. Springer, Berlin, Heidelberg, pp 333–393
- Mimura T, Dietz KJ, Kaiser W, Schramm MJ, Kaiser G, Heber U (1990) Phosphate transport across biomembranes and cytosolic phosphate homeostasis in barley leaves. *Planta* 180:139–146. <https://doi.org/10.1007/BF00193988>
- Miyamoto T, Ochiai K, Takeshita S, Matoh T (2012) Identification of quantitative trait loci associated with shoot sodium accumulation under low potassium conditions in rice plants. *Soil Sci Plant Nutr* 58:728–736. <https://doi.org/10.1080/00380768.2012.745797>
- Mohammed NAA (2018) Exploring Rice genetic resources to improve nutrient use efficiency. PhD Thesis, University of York
- Moll RH, Kamprath EJ, Jackson WA (1982) Analysis and interpretation of factors which contribute to efficiency of nitrogen utilisation. *Agron J* 74:562–564. <https://doi.org/10.2134/agronj1982.00021962007400030037x>
- Monostori I, Szira F, Tondelli A, Arendas T, Gierczik K, Cattivelli L et al (2017) Genome-wide association study and genetic diversity analysis on nitrogen use efficiency in a central European winter wheat (*Triticum aestivum* L.) collection. *PLoS One* 12(12):e0189265. <https://doi.org/10.1371/journal.pone.0189265.g004>
- Moose SP, Below FE (2009) Biotechnology approaches to improving maize nitrogen use efficiency. In: Kriz AL, Larkins BA (eds) *Molecular genetic approaches to maize improvement. Biotechnology in agriculture and forestry*, vol 63. Springer, Berlin Heidelberg, pp 65–77
- Morosini JS, Mendonça LDF, Lyra DH, Galli G, Vidotti MS, Fritsche-Neto R (2017) Association mapping for traits related to N use efficiency in tropical maize lines under field conditions. *Plant Soil* 421:453–463. <https://doi.org/10.1007/s11104-017-3479-3>
- Myles S, Peiffer J, Brown PJ, Ersoz EZ et al (2009) Association mapping: critical considerations shift from genotyping to experimental design. *Plant Cell* 21:2194–2202. <https://doi.org/10.1105/tpc.109.068437>
- Ng JMS, Han M, Beatty PH, Good A (2016) ‘Genes, meet gases’: the role of plant nutrition and genomics in addressing greenhouse gas emissions. In: Edwards D, Batley J (eds) *Plant genomics and climate change*. Springer, New York, NY, pp 149–172. https://doi.org/10.1007/978-1-4939-3536-9_7
- Ning P, Li S, Yu P, Zhang Y, Li C (2013) Post-silking accumulation and partitioning of dry matter, nitrogen, phosphorous and potassium in maize varieties differing in leaf longevity. *Field Crops Res* 144:19–27. <https://doi.org/10.1016/j.fcr.2013.01.020>
- Nisar A, Khan SU, Shah AH (2016) Screening and evaluation of wheat germplasm for phosphorus use efficiency. *Iran J Sci Technol Trans Sci* 40:201–207. <https://doi.org/10.1007/s40995-016-0085-9>
- Ochoa IE, Blair MW, Lynch JP (2006) QTL analysis of adventitious root formation in common bean (*Phaseolus vulgaris* L.) under contrasting phosphorus availability. *Crop Sci* 46:1609–1621. <https://doi.org/10.2135/cropsci2005.12-0446>
- Ortiz-Monasterio J, Manske G, Van Ginkel M (2001) Nitrogen and phosphorus use efficiency. In: *Application of physiology in wheat breeding*. CIMMYT, Mexico, pp 200–207

- Osman AM, Struik PC, Lammerts van Bueren ET (2012) Perspectives to breed for improved baking quality for wheat varieties adapted to organic growing conditions. *J Sci Food Agri* 92:207–215. <https://doi.org/10.1002/jsfa.4710>
- Pathan SI, Větrovský T, Giagnoni L, Dutta R, Baldrian P, Nannipieri P, Renella G (2018) Microbial expression profiles in the rhizosphere of two maize lines differing in N use efficiency. *Plant Soil* 433:401–413. <https://doi.org/10.1007/s11104-018-3852-x>
- Pettersson S, Jensén P (1983) Variation among species and varieties in uptake and utilization of potassium. *Plant Soil* 72:231–237. <https://doi.org/10.1007/BF02181962>
- Pingali PL (2012) Green revolution: impacts, limits, and the path ahead. *Proc Natl Acad Sci* 109(31):12302–12308. <https://doi.org/10.1073/pnas.0912953109>
- Plett DC, Holtham LR, Okamoto M, Garnett TP (2018) Nitrate uptake and its regulation in relation to improving nitrogen use efficiency in cereals. *Semin Cell Dev Biol* 74:97–104. <https://doi.org/10.1016/j.semcdb.2017.08.027>
- Poland J, Endelman J, Dawson J, Rutkoski J, Wu S, Manes Y, Dreisigacker S, Crossa J, Sánchez-Villeda H, Sorrells M, Jannink J-L (2012) Genomic selection in wheat breeding using genotyping-by-sequencing. *Plant Genome* 5(3):103–113. <https://doi.org/10.3835/plantgenome2012.06.0006>
- Presterl I, Seitz G, Landbeck M, Theimt EM, Schmidt W, Geiger HH (2003) Improving nitrogen-use efficiency in European maize; estimation of quantitative genetic parameters. *Crop Sci* 43:1259–1265. <https://doi.org/10.2135/cropsci2003.1259>
- Pszczola M, Strabel T, Mulder H, Calus M (2012) Reliability of direct genomic values for animals with different relationships within and to the reference population. *J Dairy Sci* 95:389–400. <https://doi.org/10.3168/jds.2011-4338>
- Raghuram N, Sharma N (2019) Improving crop nitrogen use efficiency. In: Moo-Young M (ed) *Comprehensive biotechnology*, vol 4. Elsevier, Pergamon, pp 211–220. <https://doi.org/10.1016/B978-0-444-64046-8.00222-6>
- Rakotoson T, Dusserre J, Letourmy J, Frouin J, Ratsimiala IR, Rakotoarisoa NV et al (2021) Genome-wide association study of nitrogen use efficiency and agronomic traits in upland rice. *Rice Sci* 28(4):379–390. <https://doi.org/10.1016/j.rsci.2021.05.008>
- Ranjan R, Yadav R (2019) Targeting nitrogen use efficiency for sustained production of cereal crops. *J Plant Nutr* 42(9):1086–1113. <https://doi.org/10.1080/01904167.2019.1589497>
- Rao IS, Neeraja CN, Srikanth B, Subrahmanyam D, Swamy N, Rajesh K et al (2018) Identification of rice landraces with promising yield and the associated genomic regions under low nitrogen. *Sci Rep* 8:9200. <https://doi.org/10.1038/s41598-018-27484-0>
- Rao IM, Terry N (1995) Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet. IV. Changes with time following increased supply of phosphate to low phosphate plants. *Plant Physiol* 107:1313–1321. <https://doi.org/10.1104/pp.107.4.1313>
- Richardson AE, Lynch JP, Peter RR, Emmanuel D, Smith FA, Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, Oberson A, Culvenor RA, Simpson RJ (2011) Plant and microbial strategies to improve phosphorous efficiency in agriculture. *Plant Soil* 349:121–156. <https://doi.org/10.1007/s11104-011-0950-4>
- Robertsen CD, Hjørtshøj RL, Janss LL (2019) Genomic selection in cereal breeding. *Agronomy* 9(2):95. <https://doi.org/10.3390/agronomy9020095>
- Safdar LB, Andleeb T, Latif S, Umer MJ, Tang M, Li X, Liu S, Quraishi UM (2020) Genome-wide association study and QTL meta-analysis identified novel genomic loci controlling potassium use efficiency and agronomic traits in bread wheat. *Front Plant Sci* 11:70. <https://doi.org/10.3389/fpls.2020.00070>
- Samal D, Kovar JL, Steingrobe B, Sadana US, Bhadoria PS, Claassen N (2010) Potassium uptake efficiency and dynamics in the rhizosphere of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), and sugar beet (*Beta vulgaris* L.) evaluated with a mechanistic model. *Plant Soil* 332:105–121. <https://doi.org/10.1007/s11104-009-0277-6>
- Sanchez PA, Logan TJ (1992) Myths and science about the chemistry and fertility of soils in the tropics. *Myths Sci Soils Tropics* 29:35–46

- Sanchez-Bragado R, Serret MD, Araus JL (2017) The nitrogen contribution of different plant parts to wheat grains: exploring genotype, water, and nitrogen effects. *Front Plant Sci* 7:1986. <https://doi.org/10.3389/fpls.2016.01986>
- Sánchez-Calderón L, López-Bucio J, Chacón-López A, Gutiérrez-Ortega A, Hernández-Abreu E, Herrera-Estrella L (2006) Characterization of low phosphorus insensitive mutants reveals a crosstalk between low phosphorus-induced determinate root development and the activation of genes involved in the adaptation of Arabidopsis to phosphorus deficiency. *Plant Physiol* 140(3): 879–889. <https://doi.org/10.1104/pp.105.073825>
- Sarkar D, Baishya LK (2017) Nutrient use efficiency. In: Naeem M, Ansari AA, Gill SS (eds) Essential plant nutrients uptake, use efficiency, and management. Springer, Cham, pp 119–146. <https://doi.org/10.1007/978-3-319-58841-4>
- Schachtman DP, Shin R (2007) Nutrient sensing and signaling: NPKS. *Annu Rev Plant Biol* 58:47–69. <https://doi.org/10.1146/annurev.arplant.58.032806.103750>
- Shabala S, Pottosin I (2014) Regulation of potassium transport in plants under hostile conditions: implications for abiotic and biotic stress tolerance. *Physiol Plant* 151(3):257–279. <https://doi.org/10.1111/ppl.12165>
- Sharma N, Sinha VB, Kumar NAP, Subrahmanyam D, Neeraja CN, Kuchi S, Jha A, Prasad R, Sitaramam V, Rghuram N (2021) Nitrogen use efficiency phenotype and associated genes: roles of germination, flowering, root/shoot length and biomass. *Front Plant Sci* 11:1–20. <https://doi.org/10.3389/fpls.2020.587464>
- Shrivastav P, Prasad M, Singh TB, Yadav A, Goyal D, Ali A, Dantu PK (2020) In: Naeem M, Ansari A, Gill S (eds) Role of nutrients in plant growth and development. Contaminants in agriculture. Springer International Publishing AG, Cham, pp 43–59
- Silva AD, Bruno IP, Franzini VI, Nerícílenes CM, Leticia B, Muraoka T (2016) Phosphorous uptake efficiency, root morphology and architecture in Brazilian wheat cultivars. *J Radioanal Nucl Chem* 307:1055–1063. <https://doi.org/10.1007/s10967-015-4282-3>
- Sims JT, Simard RR, Joern BC (1998) Phosphorus loss in agricultural drainage: historical perspective and current research. *J Environ Qual* 27(2):277–293. <https://doi.org/10.2134/jeq1998.00472425002700020006x>
- Soumya PR, BurrIDGE AJ, Singh N, Batra R, Pandey R et al. (2021) Population structure and genome-wide association studies in bread wheat for phosphorus efficiency traits using 35K wheat Breeder's Affymetrix array. *Sci Rep* 11:7601. doi: <https://doi.org/10.1038/s41598-021-87182-2>
- Spindel J, Begum H, Akdemir D, Virk P, Collard B, Redona E et al (2015) Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines. *PLoS Genet* 11:e1004982. <https://doi.org/10.1371/journal.pgen.1004982>
- Srivastava RK, Singh RB, Pujarula VL, Bollam S, Pusuluri M, Chellapilla TS, Yadav RS, Gupta R (2020) Genome-wide association studies and genomic selection in pearl millet: advances and prospects. *Front Genet* 10:1389. <https://doi.org/10.3389/fgene.2019.01389>
- Steingrobe B, Claassen N (2000) Potassium dynamics in the rhizosphere and K efficiency of crops. *J Plant Nutr Soil Sci* 163:101–106. [https://doi.org/10.1002/\(SICI\)1522-2624\(200002\)163:1<101::AID-JPLN101>3.0.CO;2-J](https://doi.org/10.1002/(SICI)1522-2624(200002)163:1<101::AID-JPLN101>3.0.CO;2-J)
- Sun X, Ren W, Wang P, Chen F, Yuan L, Pan Q, Mi G (2020) Evaluation of maize root growth and genome-wide association studies of root traits in response to low nitrogen supply at seedling emergence. *Crop J* 9(4):794–804. <https://doi.org/10.1016/j.cj.2020.09.011>
- Swamy HKM, Anila M, Kale RR et al (2019) Phenotypic and molecular characterization of rice germplasm lines and identification of novel source for low soil phosphorus tolerance in rice. *Euphytica* 215:118. <https://doi.org/10.1007/s10681-019-2443-0>
- Tang W, Ye J, Yao X, Zhao P, Xuan W, Tian Y, Zhang Y, Xu S, An H, Chen G et al (2019) Genome-wide associated study identifies NAC42-activated nitrate transporter conferring high

- nitrogen use efficiency in rice. *Nat Commun* 10(1):5279. <https://doi.org/10.1038/s41467-019-13187-1>
- Tiong J, Sharma N, Sampath R, MacKenzie N, Watanabe S, Metot C, Lu Z, Skinner W, Lu Y, Kridl J, Baumann U, Heuer S, Kaiser B, Okamoto M (2021) Improving nitrogen use efficiency through over expression of alanine aminotransferase in rice, wheat and barley. *Front Plant Sci* 12:628521. <https://doi.org/10.3389/fpls.2021.628521>
- Tollenaar M, Lee E (2011) 2 strategies for enhancing grain yield in maize. *Plant Breeding Rev* 34: 37–82. <https://doi.org/10.1002/9780470880579.ch2>
- Tong C, Shen L, Lv Y, Wang Z, Wang X et al (2014) Structural mapping: how to study the genetic architecture of a phenotypic trait through its formation mechanism. *Brief Bioinform* 15:43–53. <https://doi.org/10.1093/bib/bbs067>
- van de Wiel CCM, van der Linden CG, Scholten OE (2016) Improving phosphorus use efficiency in agriculture: opportunities for breeding. *Euphytica* 207:1–22. <https://doi.org/10.1007/s10681-015-1572-3>
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a non-renewable resource. *New Phytol* 157:423–447. <https://doi.org/10.1046/j.1469-8137.2003.00695.x>
- Veneklaas EJ, Lambers H, Bragg J, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible W-R, Shane MW, White PJ, Raven JA (2012) Opportunities for improving phosphorous use efficiency in crop plants. *New Phytol* 195(2):306–320. <https://doi.org/10.1111/j.1469-8137.2012.04190.x>
- Véry AA, Nieves-Cordones M, Daly M, Khan I, Fizames C, Sentenac H (2014) Molecular biology of K⁺ transport across the plant cell membrane: what do we learn from comparison between plant species? *J Plant Physiol* 171:748–769. <https://doi.org/10.1016/j.jplph.2014.01.011>
- Vijayalakshmi P, Vishnukiran T, Kumari BR, Srikanth B, Rao IS, Swamy KN, Surekha K, Sailaja N, Subbarao LV, Rao PR, Subrahmanyam D, Neeraja CN, Voleti SR (2015) Biochemical and physiological characterisation for nitrogen use efficiency in aromatic rice genotypes. *Field Crop Res* 179:132–143. <https://doi.org/10.1016/j.fcr.2015.04.012>
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116(5):882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Vitousek PM, Naylor R, Crews T, David MB, Drinkwater LE, Holland E, Johnes PJ, Katzenberger J, Martinelli LA, Matson PA et al (2009) Nutrient imbalances in agricultural development. *Science* 324(5934):1519–1520. <https://doi.org/10.1126/science.1170261>
- Wan TE, Xue HE, TONG YP (2017) Transgenic approaches for improving use efficiency of nitrogen, phosphorus and potassium in crops. *J Integr Agri* 16(12):60345–60347. doi: [https://doi.org/10.1016/S2095-3119\(17\)61709-X](https://doi.org/10.1016/S2095-3119(17)61709-X)
- Wang K, Cui K, Liu G, Luo X, Huang J, Nie L, Wei D, Peng S (2017a) Low straw phosphorous concentration is beneficial for high phosphorous use efficiency for grain production in rice recombinant inbred lines. *Field Crop Res* 203:65–73. <https://doi.org/10.1016/j.fcr.2016.12.017>
- Wang K, Cui K, Liu G, Xie W, Yu H, Pan J, Huang J, Nie L, Shah F, Peng S (2014) Identification of quantitative trait loci for phosphorus use efficiency traits in rice using a high density SNP map. *BMC Genet* 15:155. <https://doi.org/10.1186/s12863-014-0155-y>
- Wang LD, Liao H, Yan XL, Zhuang BC, Dong YS (2004) Genetic variability for root hair traits as related to phosphorus status in soybean. *Plant Soil* 261:77–84. <http://www.jstor.org/stable/24124282>
- Wang Z, Ma Bao-Luo YX, Gao J, Sun J, Su Z, Yu S (2019a) Physiological basis of heterosis for nitrogen use efficiency of maize. *Sci Rep* 9:18708. <https://doi.org/10.1038/s41598-019-54864-x>
- Wang H-Y, Shen Q-H, Zhou J-M, Wang J, Du C-W, Chen X-Q (2011) Plants use alternative strategies to utilize nonexchangeable potassium in minerals. *Plant Soil* 343:209–220. <https://doi.org/10.1007/s11104-011-0726-x>
- Wang X, Yan X, Liao H (2010) Genetic improvement for phosphorus efficiency in soybean: a radical approach. *Ann Bot* 106:215–222. <https://doi.org/10.1093/aob/mcq029>

- Wang QJ, Yuan Y, Liao Z, Jiang Y, Wang Q, Zhang L, Gao S, Wu F et al (2019b) Genome-wide association study of 13 traits in maize seedlings under low phosphorus stress. *Plant Genome* 12: 190039. <https://doi.org/10.3835/plantgenome2019.06.0039>
- Wang SX, Zhu YL, Zhang DX, Shao H, Liu P et al (2017b) Genome-wide association study for grain yield and related traits in elite wheat varieties and advanced lines using SNP markers. *PLoS One* 12(11):e0188662. <https://doi.org/10.1371/journal.pone.0188662>
- Welch LF, Flannery RL (1985) Potassium nutrition of corn. In: Munson RD (ed) Potassium in agriculture, ASA, CSSA and SSSA, Madison, WI, pp 647–664
- White PJ (2013) Improving potassium acquisition and utilisation by crop plants. *J Plant Nutr Soil Sci* 176:305–316. <https://doi.org/10.1002/jpln.201200121>
- White PJ, Bell MJ (2017) The genetics of potassium uptake and utilization in plants. In: Murrell TS, Mikkelsen RL (eds) Proceedings for the frontiers of potassium science conference, 25–27 January 2017. International Plant Nutrition Institute, Peachtree Corners, Rome, pp 46–65. <https://www.apni.net/k-frontiers/>. Accessed 29 May 2020
- White PJ, George TS, Gregory PJ, Bengough AG, Hallett PD, McKenzie BM (2013) Matching roots to their environment. *Ann Bot* 112:207–222. <https://doi.org/10.1093/aob/mct123>
- White PJ, Hammond JP (eds) (2008) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht
- White PJ, Karley AJ (2010) Potassium. In: Hell R, Mendel R-R (eds) Cell biology of metals and nutrients. Springer, Berlin, pp 199–224. https://doi.org/10.1007/978-3-642-10613-2_9
- Wissuwa M, Kondo K, Fukuda T, Mori A, Rose MT, Pariasca-Tanaka J, Kretzschmar T, Haeftle SM, Rose TJ (2015) Unmasking novel loci for internal phosphorus utilization efficiency in Rice germplasm through genome-wide association analysis. *PLoS One* 10(4):e0124215. <https://doi.org/10.1371/journal.pone.0124215>
- Wuebbles DJ (2009) Nitrous oxide: no laughing matter. *Science* 326:56–57. <https://doi.org/10.1126/science.1179571>
- Xu Y (2010) Molecular plant breeding. CIMMYT, Mexico
- Xu Y, Wang R, Tong Y, Zhao H, Xie Q, Liu D et al (2014) Mapping QTLs for yield and nitrogen-related traits in wheat: influence of nitrogen and phosphorus fertilization on QTL expression. *Theor Appl Genet* 127(1):59–72. <https://doi.org/10.1007/s00122-013-2201-y>
- Xu C, Zhang H, Sun J, Guo Z, Zou C et al (2018) Genome-wide association study dissects yield components associated with low-phosphorus stress tolerance in maize. *Theor Appl Genet* 131: 1699–1714. <https://doi.org/10.1007/s00122-018-3108-4>
- Yan XL, Liao H, Beebe SE, Blair MW, Lynch JM (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant Soil* 265:17–29. <https://doi.org/10.1007/s11104-005-0693-1>
- Yan H, Wenjia L, Liu X, Li G, Zhang S (2010) Comparison of rhizosphere impacts of wheat genotypes differing in phosphorus utilisation efficiency. *Canadian J Pl Sci* 90:311–317. <https://doi.org/10.4141/CJPS09005>
- Yang DL, Jing RL, Chang XP, Li W (2007) Identification of quantitative trait loci and environmental interactions for accumulation and remobilization of water-soluble carbohydrates in wheat (*Triticum aestivum* L.) stems. *Genetics* 176:571–584. <https://doi.org/10.1534/genetics.106.068361>
- Yang XE, Liu JX, Wang WM, Ye ZQ, Luo AC (2004) Potassium internal use efficiency relative to growth vigor, potassium distribution, and carbohydrate allocation in Rice genotypes. *J Plant Nutr* 27:837–852. <https://doi.org/10.1081/PLN-120030674>
- Yang N, Lu Y, Yang X, Huang J, Zhou Y, F. Ali, et al. (2014) Genome wide association studies using a new nonparametric model reveal the genetic architecture of 17 agronomic traits in an enlarged maize association panel. *PLoS Genet* 10:E1004573. doi: <https://doi.org/10.1371/journal.pgen.1004573>
- Yang X, Xia X, Zhang Z, Nong B, Zeng Y, Xiong F, Wu Y, Gao J, Deng G, Li D (2017) QTL mapping by whole genome resequencing and analysis of candidate genes for nitrogen use efficiency in rice. *Front Plant Sci* 8:1–10. <https://doi.org/10.3389/fpls.2017.01634>

- Youngquist JB, Bramel-Cox P, Maranville JW (1992) Evaluation of alternative screening criteria for selecting nitrogen use efficient genotypes in sorghum. *Crop Sci* 32:1310–1313. <https://doi.org/10.2135/cropsci1992.0011183X003200060002x>
- Zhang Z, Gao S, Chu C (2020) Improvement of nutrient use efficiency in rice: current toolbox and future perspectives. *Theor Appl Genet* 133:1365–1384. <https://doi.org/10.1007/s00122-019-03527-6>
- Zhang S, Lovdahl L, Grip H, Tong Y, Yang X, Wang Q (2009) Effects of mulching and catch cropping on soil temperature, soil moisture and wheat yield on the loess plateau of China. *Soil Tillage Res* 102(1):78–86. <https://doi.org/10.1016/j.still.2008.07.019>
- Zhang H, Uddin M, Zou C, Xie C, Xu Y, Li W (2014) Meta-analysis and candidate gene mining of low-phosphorus tolerance in maize. *J Integr Plant Biol* 56:262–270. <https://doi.org/10.1111/jipb.12168>
- Zhao K, Tung CW, Eizenga GC, Wright MH, Ali ML, Price AH, Norton GJ et al (2011) Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. *Nat Commun* 2:467. <https://doi.org/10.1038/ncomms1467>
- Ziadi N, Brassard M, Belanger G, Claessens A, Tremblay N, Cambouris AN, Nolin MC, Parent L-E (2008) Chlorophyll measurements and nitrogen nutrition index for the evaluation of corn nitrogen status. *Agron J* 100(5):1264–1273. <https://doi.org/10.2134/agronj2008.0016>
- Zörb C, Senbayram M, Peiter E (2014) Potassium in agriculture – status and perspectives. *J Plant Physiol* 171:656–669. <https://doi.org/10.1016/j.jplph.2013.08.008>