SCIENTIFIC PANEL
ON RESPONSIBLE PLANT NUTRITION

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Genetic Approaches for Improving Nutrient Use Efficiency in Crops

by the Scientific Panel on Responsible Plant Nutrition

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Content

3 Key Points
6 What is the issue?
7 Defining nutrient use efficiency for genetic improvement
12 Key steps to breed cultivars with high nutrient use efficiency
15 Case studies of crop plants whose nutrient use efficiency was genetically enhanced
22 How successful has breeding for higher nutrient use efficiency been?
24 What can be done?
29 Who needs to do what?
30 What would success look like?
31 References
34 Authors, citation and contact

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Key points

To increase global crop production without harming the environment, strategies to significantly increase nutrient use efficiency while reducing nutrient losses are essential.

This requires significant gains in nutrient use efficiencies that can only be achieved by integrating good agronomic practices with advances in fertilizer technologies and genetic improvement. Genetic strategies and crop breeding offer various opportunities to improve the potential of crops to take up or utilize plant nutrients more efficiently (Fig. 1). Various membrane proteins known as transporters mediate all these processes. Consequently, nutrient use efficiency is directly related to the properties of these transporters, including their expression levels, tissue localization, transport activity, and other characteristics.

Numerous plant traits and genes controlling the molecular processes of nutrient uptake, translocation, assimilation, and remobilization have been characterized in recent years. Despite this progress in research, there has been limited success in breeding more nutrient-efficient crop varieties. Achieving this goal will require better integration of crop genetics research with crop physiology, breeding, and agronomy, including defining realistic targets for crop improvement and rigorous field evaluation of promising candidate genes and lines.

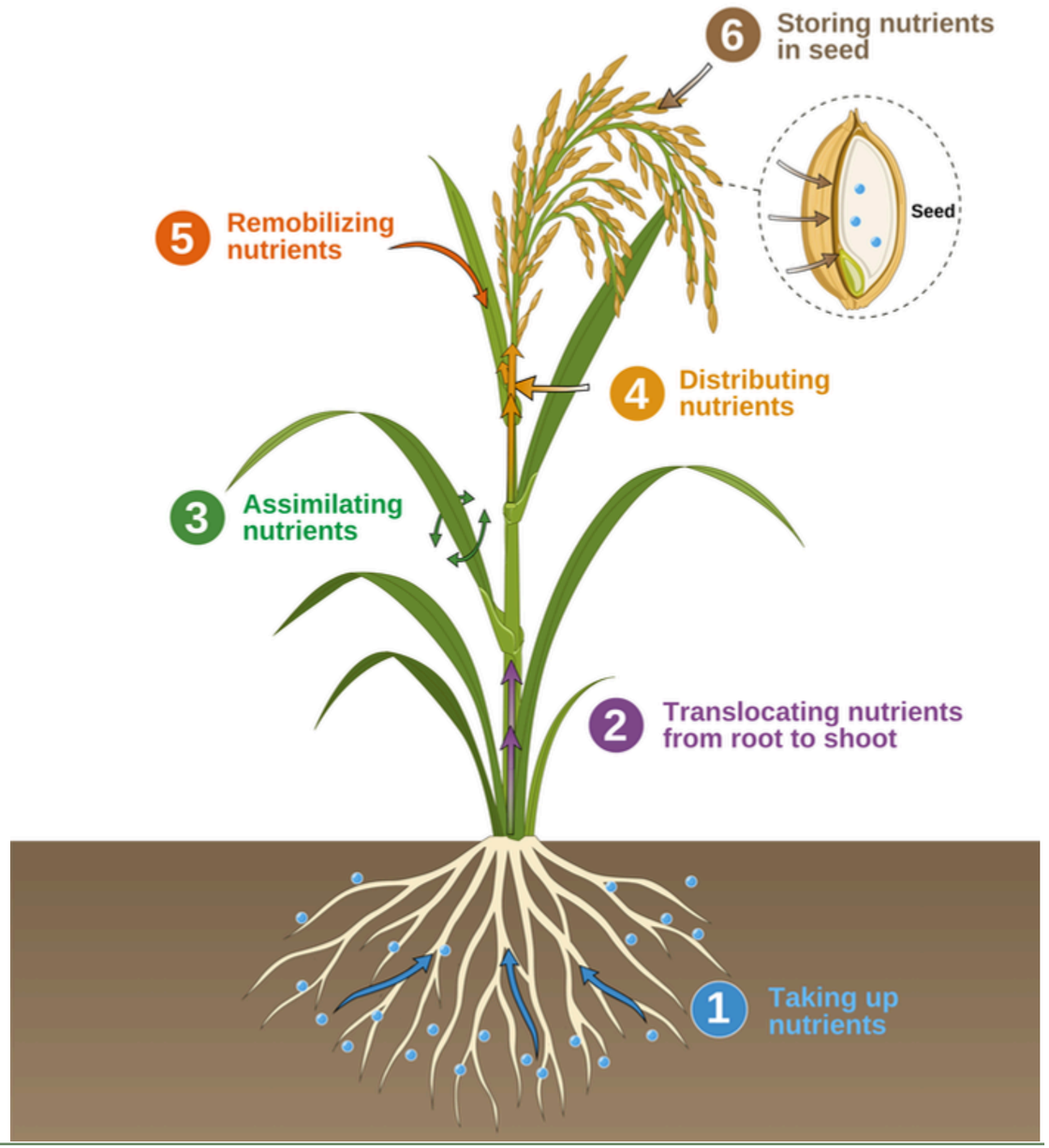

Figure 1. *Major physiological processes that provide opportunities to genetically improve the nutrient use efficiency in crops. Plants require numerous mineral nutrients for growth, development, and nutritional composition of harvested products. After these nutrients are taken up from the soil by the roots ①, they are translocated from the roots to the shoots ②. Some nutrients, such as nitrogen (N), phosphorus (P), and sulfur (S), are then assimilated in various tissues and organs ③, while others are distributed to different tissues according to their needs ④. Certain nutrients are also remobilized from older tissues to younger ones ⑤. Finally, portions of all nutrients are allocated to seeds or other organs to be harvested ⑥.*

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Glossary of key terms

Allele: Different versions or forms of a single gene (e.g., the gene is for flower color, the alleles are "red" or "white").

Gene: The basic unit of heredity; a specific sequence of DNA that codes for a specific trait.

Gene editing or genome editing (CRISPR): Technologies that allow scientists to precisely alter, delete, or add specific DNA sequences within an organism's genome. Unlike early genetic engineering techniques that randomly insert genetic material into a host genome, genome editing aims to modify a site-specific location.

Genetically modified organism: An organism whose DNA has been altered using genetic engineering techniques, often involving the transfer of genes from a different species (transgenic).

Genome: The entire genetic material or complete set of DNA of an organism.

Genotype: The specific genetic makeup or combination of alleles for an individual organism.

GWAS (Genome-Wide Association Study): A research method used to find associations between specific genetic variations and particular traits across a large population.

Locus: The specific, fixed position of a gene or marker on a chromosome.

Marker-assisted breeding (MAB): An accelerated breeding technique that uses molecular (DNA) codes to select for desirable crop traits, rather than waiting for plants to physically mature. This process includes various modern breeding procedures such as marker-assisted selection and marker-assisted backcrossing. It dramatically speeds up the development of improved crop varieties.

Molecular marker: A known, specific DNA sequence used to identify or tag the location of a gene linked to a desirable trait.

QTL (Quantitative Trait Loci): Regions of DNA that are closely linked to complex, measurable traits (such as height or drought tolerance), which are controlled by multiple genes.

Phenotype: The observable physical or biochemical characteristics of an organism, which result from the interaction between its genotype and the environment.

Proteomics: the large-scale, systematic study of the proteome, which is the entire set of proteins produced or modified by an organism or system. Because proteins are the primary functional actors in biology, proteomics is essential for understanding plant processes and their genetic control at cellular level.

SNP (Single Nucleotide Polymorphism): variation in a genetic sequence that affects only one of the basic building blocks—adenine (A), guanine (G), thymine (T), or cytosine (C)—in a segment of a DNA molecule.

Transcriptomics: the large-scale study of the transcriptome—the complete set of RNA molecules present in a cell, tissue, or organism. It reveals which genes are turned on or off, providing a dynamic snapshot of cellular function and health.

Transcription factor: A protein that binds to DNA to regulate gene expression via transcription: the process by which the genetic code generates mRNAs or small RNAs.

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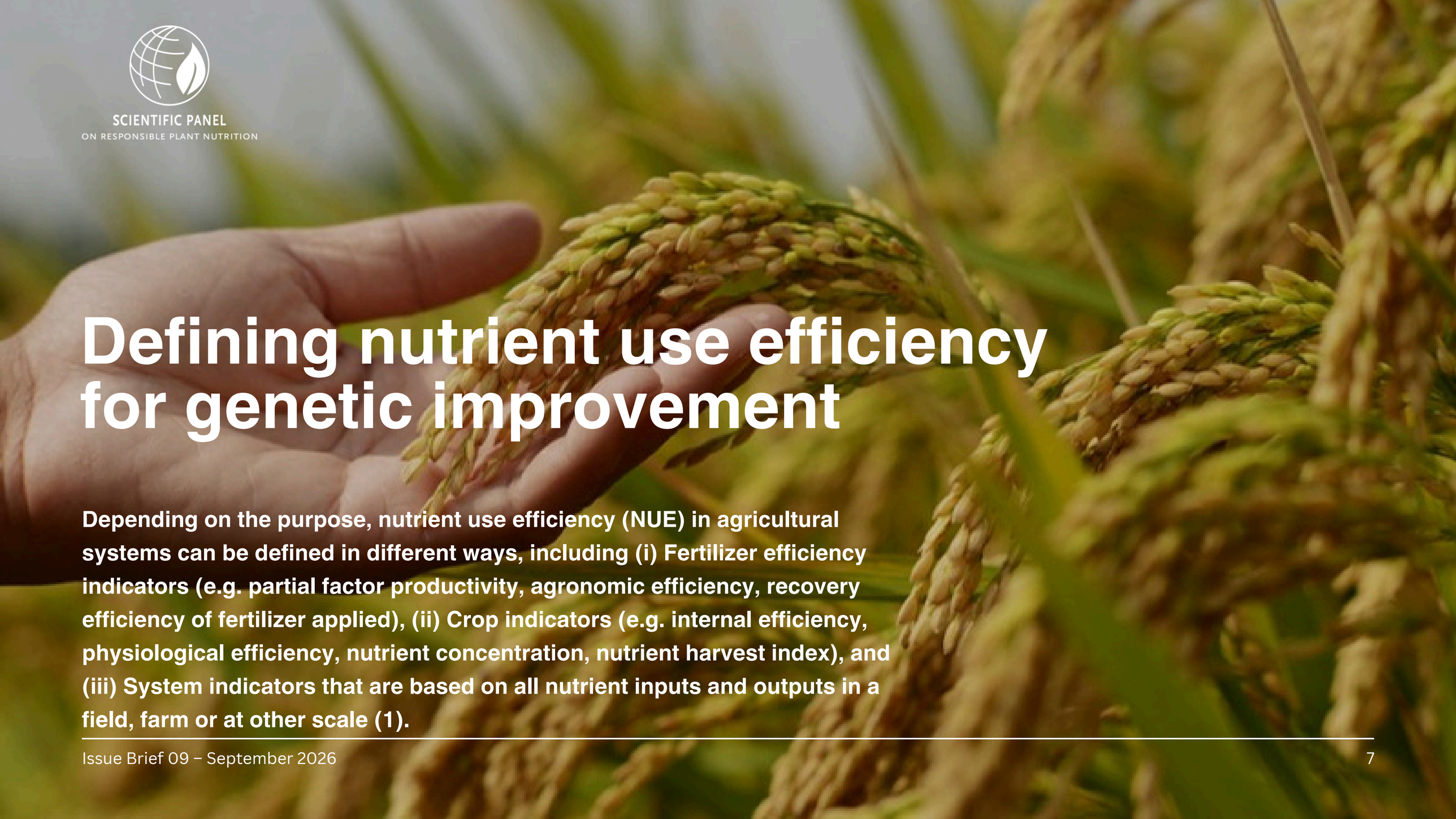
What is the issue?

Nutrient inputs from inorganic and organic fertilizers have greatly contributed to crop yield increases and global food security.

While fertilizer use remains essential to sustain high productivity for a growing world population, excessive use may lead to increased production costs, environmental pollution, biodiversity loss, or greater incidence of plant diseases. Therefore, future growth in crop production must be associated with significant increases in nutrient use efficiency (NUE) as well as reductions in nutrient losses to the environment. During the cropping season, most agricultural crops take up only 40-60% of applied fertilizer nitrogen (N), only 10-20% of applied phosphorus (P), and 40-80% of applied potassium (K). Yet, these rates depend on crop species, climate conditions, soil properties, and management practices (1–3). There is general consensus that increasing the uptake and utilization of nutrients by crops requires integrated approaches that combine improvements in site-specific agronomic practices, fertilizer technologies, and advances in genetics and crop breeding (4, 5).

Agronomic and fertilizer management practices aim to synchronize nutrient supply with crop requirement at different growth stages. Others may focus on directly reducing specific nutrient losses, such as gaseous N-losses like nitrous oxide or ammonia, or leaching of nitrate (4). Measures such as site-specific implementation of 4R nutrient management (right source, right rate, right time, right placement) (6) or enhanced-efficiency fertilizers (e.g., nitrification and urease inhibitors, controlled-release fertilizers) (7) are the primary means to improve N use efficiency and reduce N losses to the environment (1). Crop breeding, on the other hand, aims to improve the genetic potential of crops to acquire or utilize plant nutrients more efficiently (Fig. 1). It thus offers additional potential for increasing nutrient use efficiency while increasing crop production (8).

This issue brief focuses on strategies to improve the genetic potential of nutrient use efficiency in crops, with a focus on nitrogen and other macro-nutrients. Recent advances in genomics and plant science as well as new breeding technologies such as gene editing have fueled a new wave of optimism for genetic improvement of nutrient use efficiency in crops (9–12). Here, we assess the major routes being pursued and their realistic potential, and we make recommendations for how this work can be better integrated with agronomic interventions. We use rice as a main example because genomics research has advanced particularly fast in this food crop. Yet, similar conclusions can likely be drawn for other crops.



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Defining nutrient use efficiency for genetic improvement

Depending on the purpose, nutrient use efficiency (NUE) in agricultural systems can be defined in different ways, including (i) Fertilizer efficiency indicators (e.g. partial factor productivity, agronomic efficiency, recovery efficiency of fertilizer applied), (ii) Crop indicators (e.g. internal efficiency, physiological efficiency, nutrient concentration, nutrient harvest index), and (iii) System indicators that are based on all nutrient inputs and outputs in a field, farm or at other scale (1).

Here, we focus on those indicators that are useful for targeting and evaluating genetic improvement of NUE. However, we need to note, that in plant science, the following terms are often used as synonyms:

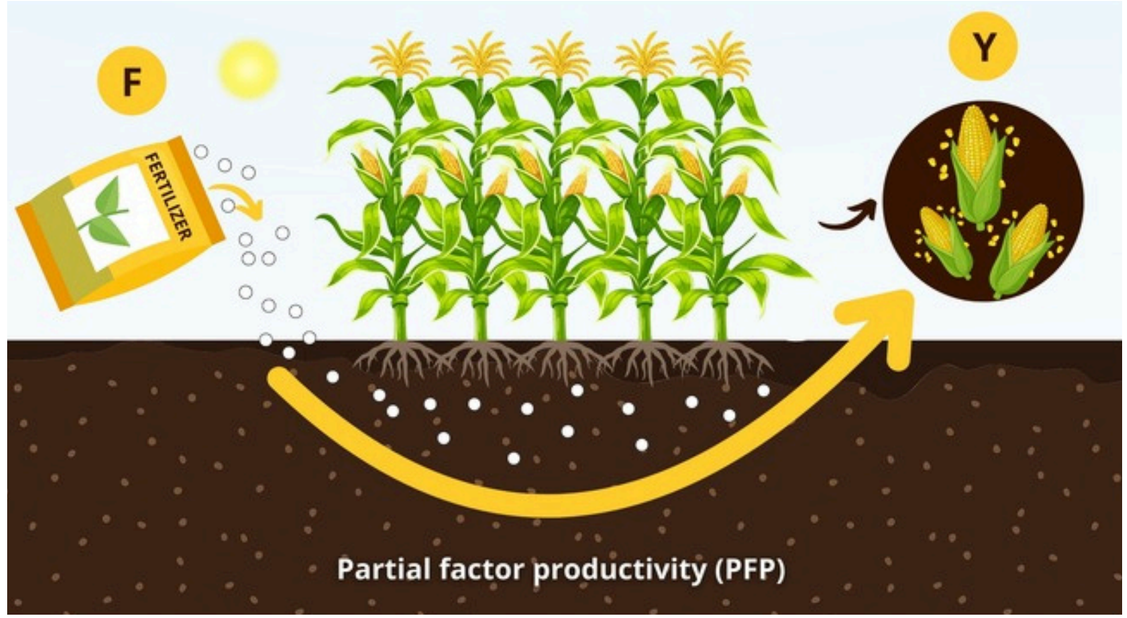
- Total nutrient use efficiency (NtUE) = PFP
- Nutrient uptake efficiency (NUpE) = RE
- Nutrient utilization efficiency (NUtE) = IE

In this Issue Brief we rely on our previously introduced terms and their definitions (1).

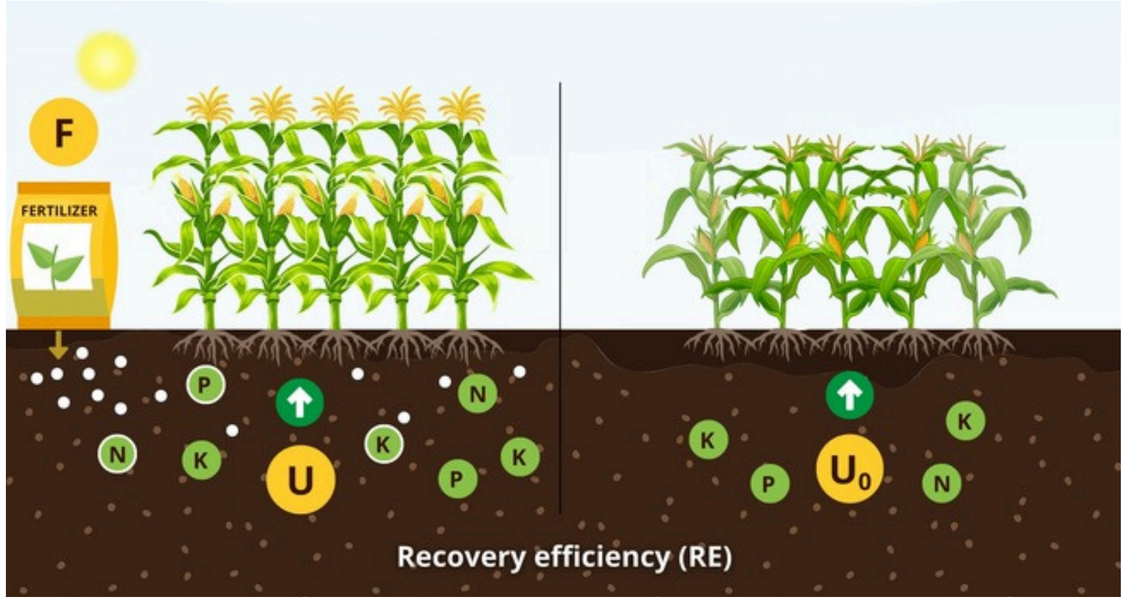
Partial factor productivity of applied nutrient: PFP = Y/F
Recovery efficiency of applied nutrient: RE = $(U-U_0)/F$
Internal efficiency of nutrients taken up: IE = Y/U
Nutrient harvest index: NHI = U_R/U

with

- Y = crop yield (kg/ha)
- F = amount of nutrient (e.g. fertilizer) applied (kg/ha)
- U = nutrient uptake with nutrient applied (kg/ha)
- U_0 = nutrient uptake without nutrient applied (kg/ha)
- U_R = nutrient amount in harvested product (e.g. grain, kg/ha)

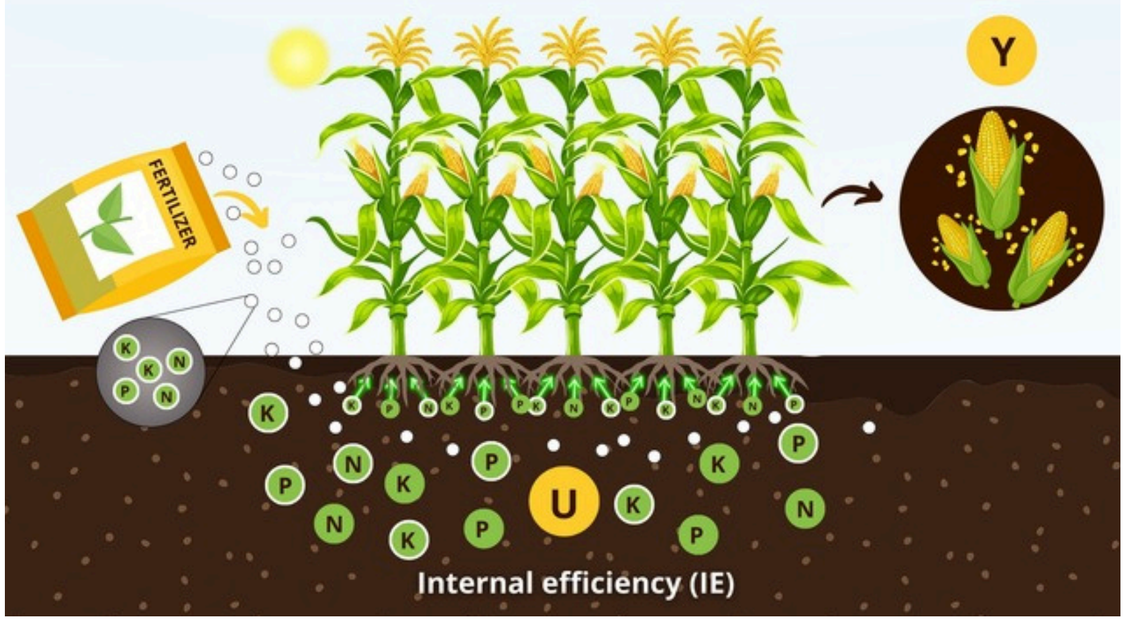


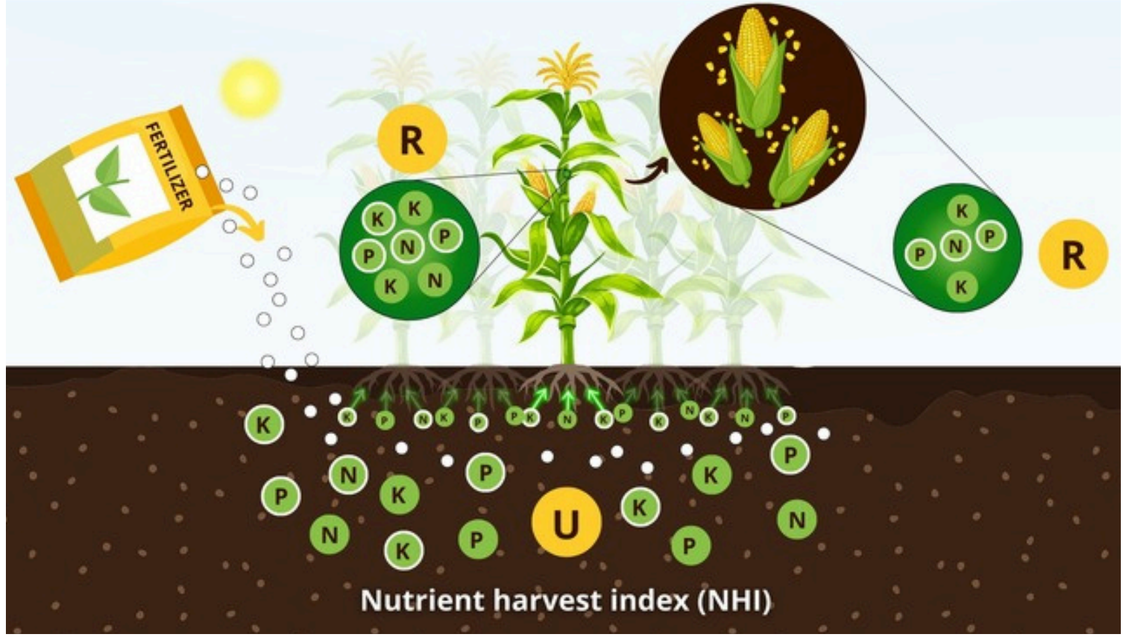
Partial factor productivity (PFP) of applied nutrient, or the crop yield harvested per unit of nutrient applied as fertilizer (e.g. kg grain per kg N applied). For farmers, PFP is a robust and economically meaningful indicator that integrates the contributions of nutrient supply from soil and other indigenous resources with the efficiency of nutrient added through fertilizers (1). From a crop improvement perspective, it is an integrating term reflecting both RE and IE (see below). Besides soil, agronomic practices and fertilizer management, PFP is also influenced by many plant processes, including nutrient uptake, root-to-shoot translocation, assimilation, distribution and remobilization (Fig. 1). The complexity of these processes suggests that – within the same genetic background – changing a single gene is unlikely to lead to large improvements in PFP, unless such changes target transcription factors controlling multiple genes involved in nutrient uptake or internal utilization.



Recovery efficiency (RE) of applied nutrient, or nutrient uptake efficiency, defined as the ratio of the increase in nutrient accumulated in the aboveground biomass of plants per unitnutrient applied as fertilizer. It expresses how much of fertilizer applied, the crop takes up, or 'recovers'. RE is influenced by factors such as root architecture, nutrient transporters, including their affinity for nutrients, abundance, activity, and regulation, root exudates, and the rhizosphere microbiome, management practices, fertilizer type and application, soil properties, and climate (1).

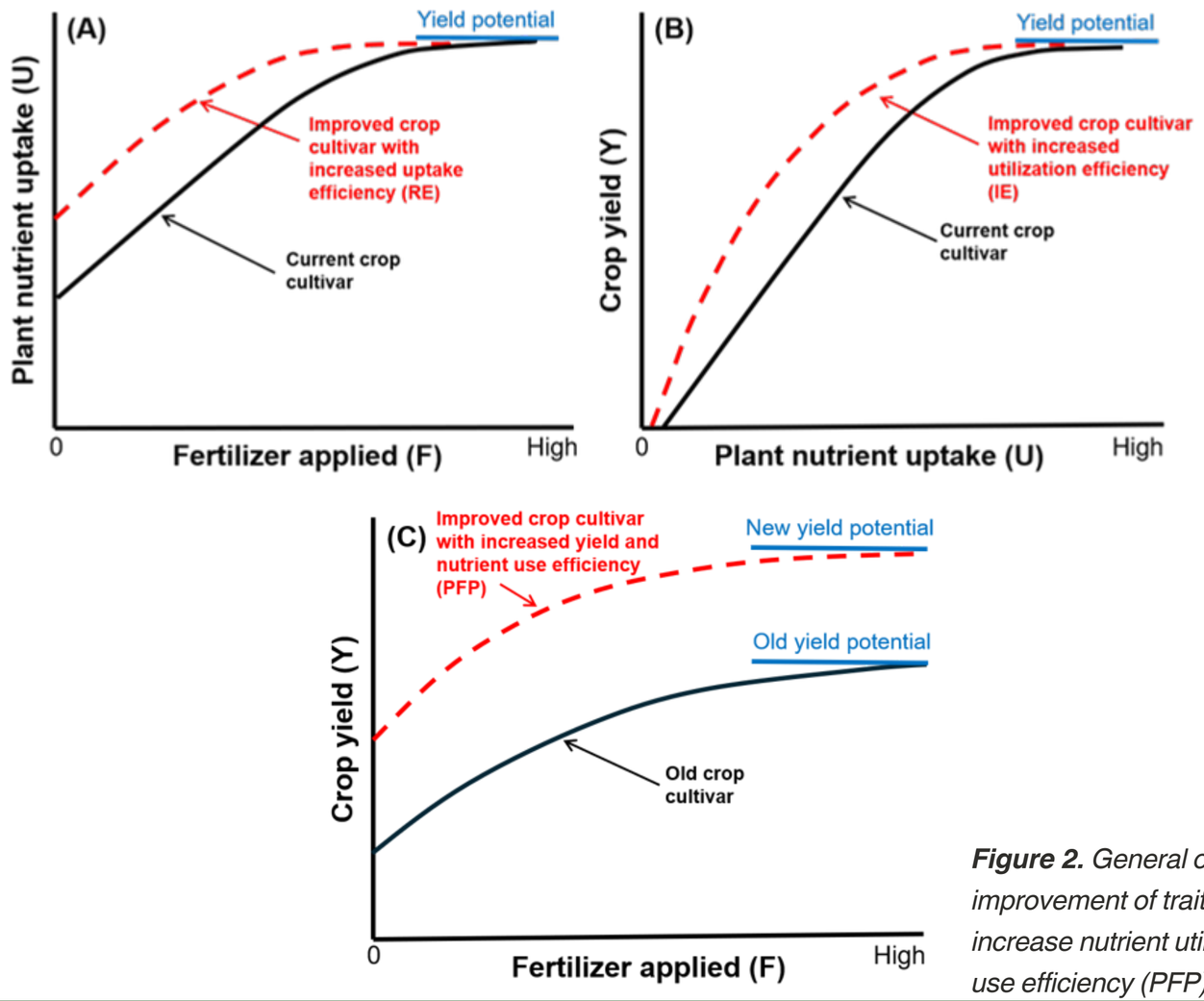
Internal efficiency (IE) of a plant nutrient, also the nutrient utilization efficiency, is calculated by dividing crop yield by the total amount of nutrients accumulated in the plant, the aboveground biomass. It expresses the ability of a plant to transform nutrients acquired from all sources, including soil and fertilizer, into economic yield. IE is determined by nutrient assimilation, root-to-shoot translocation, storage, and remobilization in plants. These processes in turn depend on the genotype, such as crop species, variety and genetic yield potential, etc., environment, and management (1). A low IE may, for example, also be caused by poor internal nutrient conversion due to other stresses, such as nutrient deficiencies, drought, heat, or diseases.





Nutrient harvest index (NHI) is defined as the proportion of nutrient in harvested crop product relative to the total amount of nutrient in above-ground crop biomass. An NHI of 0.6, for example, means that at crop maturity stage, 60% of the nutrient taken up into aboveground biomass has been allocated to the grain. Hence, 40% remains in stems, leaves, and other plant parts. The NHI is a useful indicator for crop breeding because it is directly related to nutrient partitioning, storage, and remobilization processes (Fig. 1). It also reflects the amount of nutrient in foods and feeds as harvested crop products, as well as the amount of nutrient returned to the soil as crop residues (1).

For a given crop cultivar, the attainable yield potential is defined by its general genetic characteristics and the climate during the growing season. The key nutrient-related challenge for geneticists and breeders is to improve well-adapted crop cultivars to (i) have a higher nutrient uptake efficiency (high RE, i.e. shifting the curve in Fig. 2A to the left) and/or (ii) have a lower internal nutrient requirement per unit yield (high IE, i.e. shifting the curve in Fig. 2B to the left). This can be achieved by altering crop traits associated with nutrient uptake (RE), or by genetically improving traits that improve nutrient translocation, remobilization, or storage (IE). Yet, these interventions are not to compromise crop yield, agronomic fitness, tolerance to abiotic or biotic stresses, and the desired quality of the harvested crop product.



Since the "Green Revolution" period (1950s-1970s), crop yield potential and harvest index, the proportion of the above ground biomass (in the case of cereals) in the grain, could be increased immensely in major food crops. Achieving this required breeding for traits such as short plant height (e.g. in wheat, rice, barley), more erect plant stature, and adaption to higher plant populations, greater sink size, and shorter growth duration. The resulting semi-dwarf phenotypes have increased harvest index, are more lodging-resistant, and can be harvested more efficiently (13). They are also more responsive to fertilizers.

Any such quantum leap in yield potential results in an overall NUE, or PFP, increase, as illustrated in Figure 2C, i.e. more grain produced per unit nutrient applied. This increase in PFP is a combination of increased NHI, RE, and IE, although the proportional contributions of each may vary. However, modern crop varieties have already been bred for high yield potential, whereas further increases in yield potential are likely to be modest (14). Some improvements in yield potential and NHI are still possible, but the main challenge now lies in genetically improving RE and IE, and ensuring that agronomy practices are adapted to take advantage of such gains.

Figure 2. *General options to genetically improve the crop nutrient use efficiency: A - genetic improvement of traits that increase nutrient uptake efficiency (RE); B - genetic improvement of traits that increase nutrient utilization efficiency (IE); C – genetic improvement of yield potential and overall nutrient use efficiency (PFP), due to improved uptake and utilization efficiency and nutrient harvest index.*

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Key steps to breed cultivars with high nutrient use efficiency

There are at least three general steps for developing crop varieties with improved nutrient use efficiency.

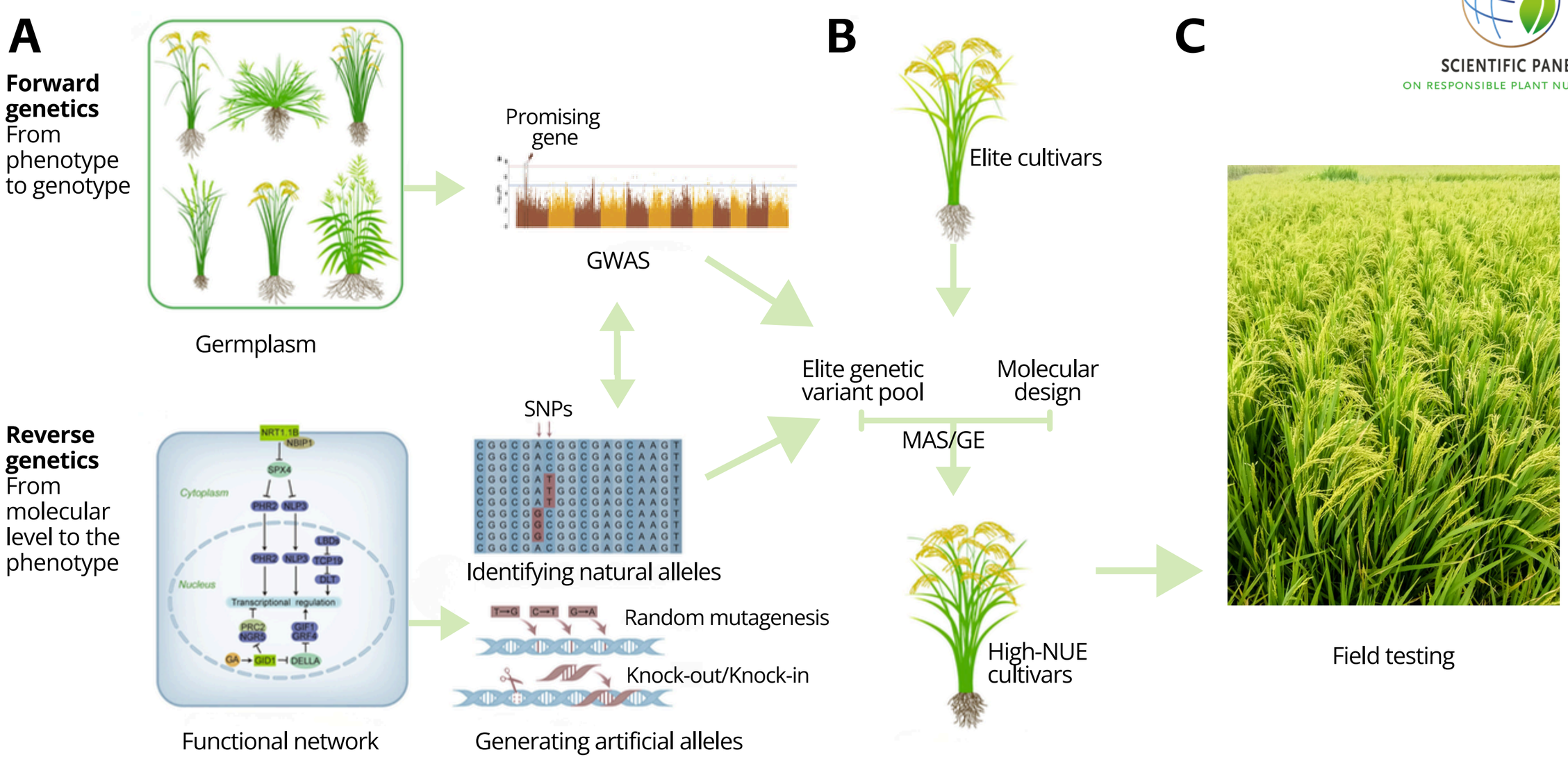

***Figure 3**. Three steps for breeding cultivars with high nutrient use efficiency. A: Identification of genes/alleles with high RE and/or IE; B: Introgression of favorable genes/alleles into elite cultivars using molecular marker-assisted selection or gene editing; C: Field testing under different conditions. Modified from (15).*

1. Identifying useful genes/alleles for higher nutrient uptake and/or utilization efficiency

Modern breeding programs have primarily selected for high yield under ample fertilizer supply, resulting in the loss of many valuable NUE-related genes/alleles. Screening diverse genetic resources (e.g. different accessions held in gene banks, existing breeding lines, specially created populations, wild relatives) can identify superior NUE alleles through approaches such as quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), marker-assisted mapping, transcriptomics, and proteomics (Fig. 3A). Reverse genetics, i.e. from genotype to phenotype, may also be used to identify genes that are important to NUE (Fig. 3). This approach is particularly useful when leveraging knowledge gained from research on model plant species, such as rice or Arabidopsis thaliana, to other crop species.

2. Introducing identified genes/alleles into elite cultivars

Once superior genes or alleles are identified, they can be introduced into high-performing elite cultivars that are adapted to local conditions and markets (Fig. 3B). This can be achieved through:

- Genetic engineering: overexpression, knockout of target genes, or genome editing
- Marker-assisted selection breeding (MAB)

Genome editing technologies enable precise modification of NUE-related genes, potentially accelerating breeding progress. However, transgenic approaches face public acceptance challenges, while MAB, though faster than conventional breeding, still requires multiple generations to breed stable lines with the desired traits.

3. Field evaluation

Rigorous field testing is essential to confirm NUE improvements (Fig. 3C), and, depending on the genetic change targeted, its components, such as uptake efficiency or utilization efficiency. Evaluations should be conducted across multiple locations and seasons, and under various fertilizer application rates to ensure robust performance. Accurate measurements and NUE calculations must be performed under these varied conditions.

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Case studies of crop plants whose nutrient use efficiency was genetically enhanced

1. Nitrogen use efficiency

Extensive research has been conducted on improving N use efficiency, particularly in rice, a staple crop for half the world's population (15). Field research has demonstrated substantial genetic differences among subspecies of rice. For example, field experiments in the Zheijiang province of China revealed that *japonica* rice had an average IE of 53 kg grain/kg N taken up, whereas *japonia x indica* rice hybrids averaged IE of 67 kg grain/kg N (16). The key question is, however, whether N use efficiency can be increased within each subspecies, and in widely grown rice cultivars.

Screening rice varieties for N use efficiency has a long history (17), with many studies leveraging natural genetic variations. Research in the 1980s and 1990s demonstrated significant genetic differences (18), including rice varieties or breeding lines that were agronomically superior and nitrogen-efficient (19). Such varietal differences in RE, IE, or NHI were found to be larger at low soil N levels and became smaller with increasing fertilizer addition. Although deemed promising, these early results had little impact on rice breeding. The possibility of incorporating genes for symbiotic nitrogen fixation into rice was also discussed at that time (17), a line of research that continues to this day. Later on, transgenic approaches were attempted, such as the tissue-specific expression of alanine aminotransferase - an enzyme with a key role in carbon and nitrogen metabolism in plants (20), but without commercial breeding success.

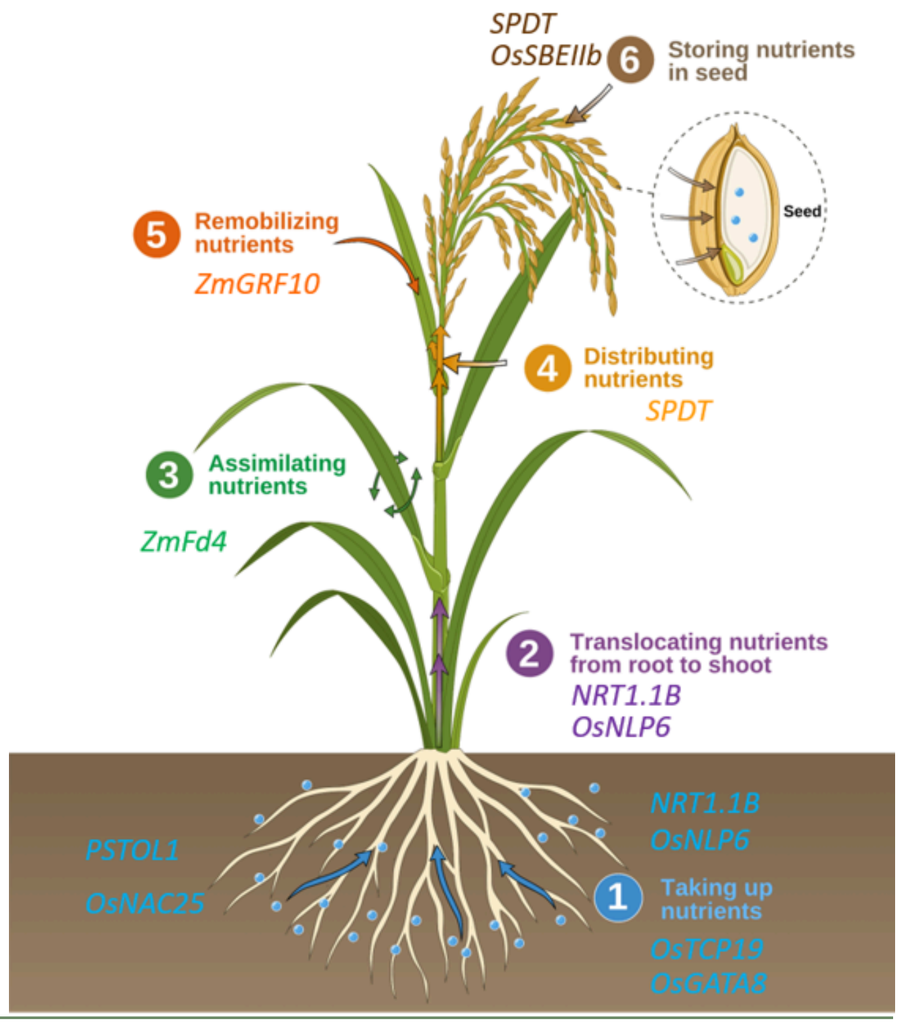


***Figure 4**. Examples of genes that enhance nutrient use efficiency and their intended target processes in the plant, as discussed in this brief.* ***Nitrogen**:* NRT1.1B *(elite allele* NRT1.1B-*indic) (22),* OsTCP19 *(*OsTCP19-*H) (23),* OsGATA8 *(*OsGATA8-*H) (24),* OsNLP6 *(*OsNlP6-^{hap11}*) (25),* ZmFd4 *(*ZmFd4^{Hap1}*) (26),* OsSBEIIb *(starch & protein) (27);* ***Phosphorus**:* PSTOL1 *(over-expression) (28), SPDT (loss of function) (29),* ZmGRF10 *(*ZmGRF10^{hap2}*) (30);* ***Potassium**:* OsNAC25 *(OsNAC25 ^{Hap1}) (31).*

In recent years, rapid advances in plant science methodologies (21), including genome analyses and functional characterization, have vastly improved the ability to discover as well as manipulate specific genes or whole crop traits controlled by multiple genes. Here, we discuss some examples that, relying on different modes of action, were shown to enhance N use efficiency (Fig. 4). Their effects in terms of enhancing N use efficiency and grain yield differ with target genes, nutrient application rates, and other factors.

Increased uptake and root-to-shoot transport of nitrate in rice

Asian cultivated rice consists of two main subspecies, indica and japonica. Indica varieties generally exhibit higher nitrate (NO_3^-) uptake and N uptake efficiency than japonica varieties. Hu et al. (22) discovered that this difference is attributed to allelic variation in the nitrate transporter gene *NRT1.1B* (*OsNPF6.5*). Compared with the japonica allele of *NRT1.1B*, the indica allele is more efficient in the uptake and root-to-shoot transport of nitrate. It also shows greater transcriptional upregulation of nitrate-responsive genes. Introducing the indica *NRT1.1B* allele into japonica varieties through breeding or transgenic approaches significantly enhanced grain yield and RE in field trials under varying nitrogen application rates.

High tillering under low N in rice

Another breakthrough came with the discovery of *OsTCP19*, which encodes a transcription factor that negatively regulates tillering in response to nitrogen availability (23). Increasing the nitrogen application rate generally promotes tillering in rice, but the response varies among different rice varieties. Tillering response to increasing nitrogen rate from low (50 kg N/ha) to moderate/high (150 kg N/ha) is a useful indicator of N use efficiency. Using this index, Liu et al. (23) identified a locus with a strong influence on tillering response to nitrogen; they then cloned the causative gene *OsTCP19*. Rice varieties with a high tillering response to nitrogen possess the allele OsTCP19, named *OsTCP19-H*, that is less responsive to nitrogen, and thus less able to suppress tillering. In contrast, rice varieties without that insertion/deletion in the *OsTCP19* promoter showed a higher response in gene expression and thus greater suppression of tillering. Intriguingly, modern high-yielding rice cultivars largely lost the *OsTCP19-H* allele, likely a result of selecting variants with only few tillers, since too many unproductive tillers at high nitrogen rates reduce grain yield. Hence, modern high-yielding rice cultivars do not produce enough tillers at low to moderate nitrogen rates resulting in relatively low N use efficiency. When the *OsTCP19-H* allele was reintroduced into elite varieties, grain yield and NUE were significantly increased under low to moderate nitrogen levels.

Coordinating N uptake and tillering in rice

Further expanding on nitrogen regulatory mechanisms, Wu et al. (24) identified *OsGATA8*, encoding a transcription factor that plays a dual role in regulating nitrogen uptake and tillering. OsGATA8 is a negative regulator of the ammonium transporter gene *OsAMT3.2* as well as *OsTCP19*, whose gene product suppresses ammonium uptake and promotes tillering. Rice varieties or isogenic lines possessing an allele of *OsGATA8* with a deletion in the promoter - named *OsGATA8*-H - exhibit lower expression of OsGATA8, resulting in higher expression of *OsAMT3.2* and *OsTCP19*. These varieties or isogenic lines take up more ammonium under low nitrogen conditions and form fewer nonproductive tillers, thus a higher proportion of productive tillers, under high nitrogen conditions. Introducing the *OsGATA8*-H allele into modern rice cultivars increased grain yield and RE at both low and high nitrogen application rates. Furthermore, the superior *OsGATA8*-H and *OsTCP19*-H alleles are rarely present together in rice varieties. Combining these two alleles into the same cultivar could further increase N use efficiency and yield under a broad range of nitrogen levels.

A transcription factor as a key regulator of N use efficiency in rice

Recent work in rice showed that *OsNLP6*, encoding a NIN-like protein (NLP) transcription factor, was associated with N use efficiency (25). NIN-like proteins are key regulators involved in nitrate signaling, NUE, and biological nitrogen fixation (32). *OsNLP6* regulates the uptake and root-to-shoot translocation of nitrate, but not ammonium. Hence, differently from *OsTCP-19* and *OsGATA8*, the gene product of *OsNLP6* is a positive regulator of N use efficiency. An elite allele, DF114^{Hap11}, with higher expression of *OsNLP6* was identified and found to be present mainly in indica rice varieties from southeast Asia. Introducing *OsNLP6*^{HapII} into *japonica* rice resulted in increased N uptake efficiency and grain yield at low and higher N application rates (Fig. 5), but no improvement in the internal utilization efficiency (not shown).

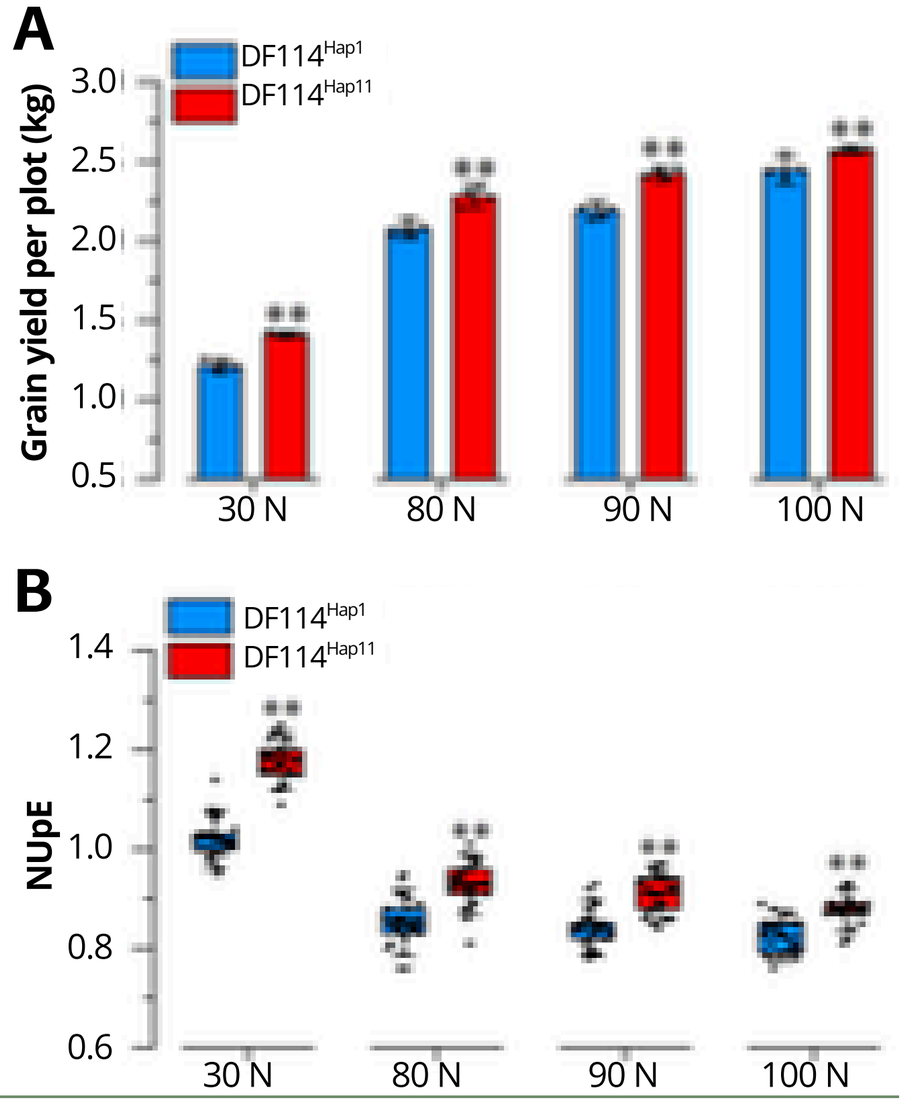


Figure 5. *Effect of introgression of the elite allele* OsNLP6 *(DF114^{Hap11}) on grain yield (A) and N uptake efficiency (B) of rice grown at different N application rates. Adopted from Xin et al. (25)*

Enhancing nitrate assimilation in maize

In maize, *ZmFd4*, encoding a ferredoxin protein, was found to be a major contributor to natural variation in shoot nitrate concentration (26). ZmFd4 interacts with nitrite reductases in chloroplasts, boosting their enzymatic activity for efficient nitrate assimilation. Maize lines in which *ZmFd4* was knocked out exhibited higher nitrate assimilation and grain yield under nitrogen-limiting conditions (0 or 34.5 kg N/ha). But there was no effect at normal rates of nitrogen application (138 kg N/ha).

Dual regulation of N and P utilization in wheat

In wheat, Liu et al. (33) identified *TaTCP6*, encoding a transcription factor that enhances both nitrate uptake/utilization and phosphorus starvation responses. The gene product of *TaTCP6* activates nitrogen utilization genes and interacts with *TaPHR2*, which encodes a key regulator of phosphate uptake, thus improving phosphorus-use efficiency. Overexpressing *TaTCP6* in wheat increased grain yield, highlighting its dual role in optimizing N and P utilization.

Increasing protein content in cereals

More recently, improving both the quantity and quality of cereal protein has become increasingly recognized as an opportunity to enhance human health while reducing reliance on environmentally intensive animal-based foods (34). For example to make bread, wheat requires high protein levels, particularly in environments with declining N use (35). Protein content is usually negatively correlated with starch accumulation and grain yield. Several genes significantly impact grain protein content and evidence is emerging that the negative link between protein content and grain yield can be overcome (35). For example, in rice, the starch-branching enzyme IIb OsSBEIIb plays a key role in determining amylopectin structure and starch digestibility. Kor et all. (27) gene-edited *OsSBEIIb* in indica cultivar IR64, which increased resistant starch and grain protein levels by up to 10%. However, these increases also resulted in poorer eating quality and some agronomic trade-offs, indicating that more research is needed to convincingly achieve the intended targets. Overall, however, genetic strategies to increase grain protein in cereals is an important route for crop breeding (35) that could also result in increased NHI, IE, and PFP of fertilizer nitrogen.

2. Phosphorus use efficiency

Due to strong fixation of phosphate in soil, P fertilizer recovery efficiency is typically low (10–20%), depending on soil type and other factors (2). That's why genetic improvement strategies aim to increase P uptake efficiency, enhance remobilization of P stored in soil, and reduce P content in grains (12).

Enhancing early root growth in rice and other cereals

Gamuyao et al. (28) identified *PSTOL1* (Phosphorus Starvation Tolerance 1), a gene that is absent in modern rice varieties but present in phosphorus-efficient, locally adapted, traditional varieties. Overexpressing *PSTOL1* in elite rice significantly improved grain yield in phosphorus-deficient soils by promoting early root growth, enabling plants to access more phosphorus and other nutrients.

The function of PSTOL1 in rice inspired its application in wheat. Milner et al. (36) overexpressed the rice *OsPSTOL1* gene in wheat, and thus improved yields under both low-phosphate and low-nitrogen conditions, suggesting its broad utility in cereal crops.

Enhancing phosphorus remobilization in maize

Crop plants can remobilize certain nutrients, including N and P, from senescing or mature vegetative tissues to developing organs such as young leaves and grains, thereby increasing the internal nutrient utilization efficiency. In maize, for example, the gene product of *ZmGRF10* negatively regulates genes involved in degrading substrates containing organic phosphorus (30). Consequently, knocking out this gene enhances tolerance to low P conditions by promoting internal P remobilization. In some maize varieties, single nucleotide polymorphisms (SNPs) in the promoter region of *ZmGRF10* resulted in reduced transcriptional activity without altering gene function. These findings make this locus a promising target for breeding varieties with higher phosphorus use efficiency.

Modifying phosphorus allocation to grains

In cereal crops, the majority of N and P taken up is ultimately allocated to the seeds. In gramineous species such as rice, transporters expressed in the nodes mediate this distribution. Yamaji et al. (29) demonstrated that *SPDT*, a gene encoding a phosphate transporter, plays a key role in directing P to rice grains. Under P-limited conditions, knocking out *SPDT* impaired the growth of developing tissues. However, under normal or high P supply, disrupting this gene reduced grain P allocation, leading to a 20–30% decrease in grain phytate content. Given that P fertilizer application is essential for maintaining high grain yields, *SPDT* knockout offers dual benefits of a lower phytate content: it (i) improves the bioavailability of iron (Fe) and zinc (Zn) for human nutrition and (ii) mitigates environmental pollution risks, particularly eutrophication of waterbodies (37). Moreover, because more P remains in the straw, this approach could indirectly reduce the need for fresh P fertilizer inputs if straw is returned to soil. As a result, *SPDT* has been identified as a target for breeding low-phytate rice varieties.

3. Potassium use efficiency

The internal requirements of crops for potassium vary widely among crop species (Fig. 6), crop cultivars, and yield levels (38). This is mainly because the composition of harvested products differs and potassium has both specific and unspecific physiological functions. Some of these can also be substituted for by other mineral elements such as sodium.

Although much research has focused on K transport and signaling in plants, less attention has been paid to breeding for K use efficiency (39). Manipulating root architecture together with K transport and distribution within the plant can potentially improve K use efficiency (40). Such varieties should, for example, take up, distribute, absorb, and utilize K more efficiently, especially in soils with lower K levels (39). Genotypes with greater IE, on the other hand, would be able to redistribute more K from older to younger tissues and reduce vacuolar K concentration, while maintaining an appropriate K concentration in metabolically active subcellular compartments (41).

Improving potassium uptake in rice

Potassium is an important nutrient for rice, but it is also increasingly limiting rice yields in Asia (42). In contrast to nitrogen, japonica rice varieties typically exhibit higher tolerance to low K than indica varieties. Wang et al. (31) identified *OsNAC25*, encoding a transcription factor regulating the expression of genes involved in K uptake. The *japonica* allele of *OsNAC25* enhanced K accumulation under low-K soil conditions. Introducing this allele into an indica rice variety improved plant growth and K uptake under low K conditions, demonstrating its potential for breeding K-efficient crops.

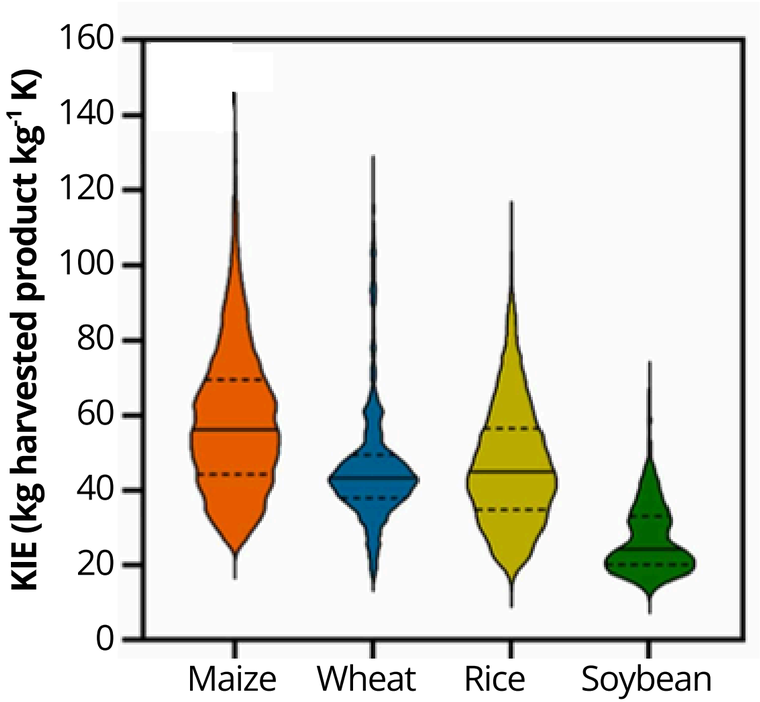


Figure 6. *Variation in potassium internal efficiency (KIE, amount of grain produced per unit K uptake) in maize, wheat, rice, and soybean. The horizontal lines inside the violins represent the median (solid line) and the 25th and 75th percentiles (dashed lines). Adapted from Carciochi et al. (38).*

SCIENTIFIC PANEL
ON RESPONSIBLE PLANT NUTRITION

How successful has breeding for higher nutrient use efficiency been?

Broadly speaking, despite much progress in molecular genetics research, progress in breeding new crop varieties with direct improvements in nutrient use efficiency has been slow. This is for example mainly due to the difficulty of breeding for N use efficiency. Genetic control must consider the complex physiological and metabolic factors influencing N uptake from soil, as well as N utilization efficiency and allocation within the plant (Fig. 1). These processes involve numerous biochemical pathways and feedback mechanisms that are highly sensitive to environmental conditions, and are thus controlled by many genes (43, 44).

Although there is consensus on the need to increase NUE through breeding, NUE has generally not been a major target of dedicated breeding programs. NUE has however, been improved indirectly by selecting for yield in many crops (43, 45). For example, deploying the reduced-height semi-dwarfing genes was a crucial component of the 'Green Revolution'. Thus, improving yield potential of wheat was due to an increased harvest index, lodging resistance, and fertilizer use efficiency (46). Also, maize breeding in North America led to an increase of the NHI of nitrogen from 58% in 1946 to 69% in 2015 (47). Several studies in Mexico and France have shown modest breeding improvement of N use efficiency in wheat (43). In oilseed rape, breeding increased N use efficiency in modern varieties, including N uptake efficiency at high N levels (48). In Japan, the large-grain rice variety Akita 63 also showed superior N uptake and utilization efficiency (49).

More recently, several seed companies in China have started to breed new rice hybrids specifically with some of the N use efficiency genes (Figure 4.) The *OsTCP19* gene was already introduced into about 30 hybrid rice cultivars, which have been grown on several million hectares. Nitrogen fertilizer trials conducted with such hybrids have demonstrated increases in nitrogen partial factor productivity of about 13-15% under medium and high N conditions. Other breeding trials also focus on optimizing the *OsGATA8* gene, but no cultivars have been released yet. These are among the first examples of newly discovered N use efficiency improving genes being used in commercial crop breeding, indicating significant potential to harness.

What can be done?

Over the past few decades, many scientific papers have claimed that modifying one or several genes may result in substantial increases in crop yield, nutrient use efficiency, or other outcomes. Although these research projects have contributed to important insights into molecular biology and gene discovery, there are also growing concerns that many of the claims are exaggerated and not based on rigorous field evaluation (50). Many studies were based on pot experiments, with only limited field evaluation, or the research was not done in the right genetic background. Plant nutrients and NUE are also often measured and calculated incorrectly.

Realistic targets and expectations

There is clearly scope to genetically improve nutrient uptake and utilization in crops, while taking into account biological limits on crop nutrient requirements (51). Nevertheless, even modest increases (5-10%) in RE and/or IE, or a combination of both, could have big impacts. These hypothetical, and yet realistic, scenarios could look as follows:

- **Baseline**: The average rice yield across different growing regions and seasons in Asia is about 5200 kg/ha and, on average, farmers apply about 100 kg N/ha fertilizer. Crop N uptake is about 87 kg N/ha, with a fertilizer N recovery efficiency (RE) of about 40%, internal efficiency (IE) of about 60 kg grain/kg N taken up and an average nitrogen harvest index (NHI) of 60% (3, 52).
- **Scenario A - increasing RE by 10%**: Breeding for root N uptake traits could improve N uptake efficiency by 10% (from 40 to 44%) without changes in yield and IE (or NHI). This would result in 17 kg N/ha less fertilizer N required for the same yield level, and a 20% increase in PFP, from 52 to 62 kg grain/kg fertilizer N compared to the baseline. Across Asia, around 2.5 million tons of fertilizer N could be saved each year.
- **Scenario B - increasing IE by 10%:** Breeding for traits that increase N distribution, remobilization or storage in grain could improve N utilization efficiency by 10% (from 60 to 66 kg grain/kg N uptake) without changes in yield and RE. This would result in 28 kg N/ha less fertilizer N required, and a 39% increase in PFP, from 52 to 72 kg grain/kg fertilizer N compared to the baseline. Across Asia, 4.2 million tons of fertilizer N could be saved without reducing rice production.

Scenarios A and B demonstrate the general potential for genetic improvements. A common misconception is, however, that the goal of improving NUE is to reduce fertilizer application, and therefore cost and greenhouse gas emissions. The real challenge is to increase the amount of grain produced per unit of nutrient applied while increasing grain yield to produce more food for a growing population. There are minimum requirements for nutrients in the harvested products, and hence higher yields demand greater nutrient input – primarily from fertilizers – but with greater efficiency of uptake and utilization by the plant. Scenario C represents that case:

- **Scenario C - increasing grain yield, RE and IE each by 10%:** Genetic improvement and better agronomic practices could together improve both RE and IE by 10% each with an additional yield increase of 10% (from 5.2 to 5.7 t/ha). This would result in better N uptake and utilization, supporting food security and requiring 17 kg N/ha less fertilizer N than the baseline, all while achieving a 32% increase in PFP (from 52 to 69 grain/kg fertilizer N).

Table 1. Theoretical scenarios for outcomes of genetic improvement strategies as outlined in the text.

Scenario	Yield (t/ha)	RE (%)	IE (kg grain/kg N)	Fertilizer N (kg/ha)	PFP (kg grain/kg N)	N saved (Mt/yr)
Baseline	5.2	40	60	100	52	
A	5.2	44	60	83	62	2.5
B	5.2	40	66	72	72	4.2
C	5.7	44	66	83	69	2.5

Gene discovery: exploring superior alleles in wild relatives and landraces

Most NUE-enhancing genes (alleles) found so far are induced at low-nutrient conditions, probably because they have evolved to enhance survival under nutrient scarcity. Many of them become ineffective at high-nutrient levels, suggesting that high fertilizer use in modern agriculture may mask their NUE-enhancing functions (53). This creates a tradeoff between achieving high yields and increasing NUE. Alleles, such as *OsGAT8-H*, that can improve NUE under a broad range of nutrient supply conditions are particularly useful.

Modern breeding has prioritized high yields under high nutrient inputs. Therefore some genes (or alleles) related to high NUE might have gotten lost during modern breeding processes. To recover these traits, wild relatives and traditional landraces—which may harbor untapped genetic diversity—should be screened for superior NUE alleles. Advanced genomic tools, such as GWAS, pan-genome analysis, etc, can identify such NUE-associated genes/alleles (Fig. 3). One should note that functional validation is essential before breeding applications. Not all genes involved in nutrient uptake, translocation, distribution, or redistribution are suitable targets; priority should be given to those with demonstrated agronomic value under a range of realistic production conditions. Efficient off-station screening strategies are needed for that, along with more robust environmental characterization data to empower Genotype x Environment x Management assessments.

Targeted breeding

Crop breeding has shifted to data-driven, targeted breeding strategies with diverse product design and development. These often harness modern tools and technologies such as gene editing, genomic selection, speed breeding, and environment-specific field testing to accelerate genetic gain and swiftly replace crop cultivars through effective seed systems (54). The new era is one of intelligent design, supported by advances in genomics and artificial intelligence (AI) (55). Such genomics-assisted breeding relies on new approaches that fast-track targeted manipulation of allelic variation for creating novel diversity and facilitate their rapid and efficient incorporation into crop improvement programs (56).

Yield enhancement will remain the main breeding goal and it is unlikely that NUE traits per se would have commercial viability independent from yield (57). However, NUE-related traits should be more systematically included in breeding profiles for optimal product placement, particularly in crops and cropping systems where significant gains could be achieved. Promising candidate genes/alleles should be introgressed into elite cultivars via marker-assisted selection or gene editing methods, such as CRISPR-Cas9. The resulting lines should be rigorously tested in the targeted market segments, the local environments. Longer-term studies are also needed to assess agronomic performance and sustainability under specific management conditions, including proper measurement of NUE indicators, to quantify how genetic improvement and agronomic practices contribute to improving NUE.

Gene pyramiding for multi-nutrient efficiency

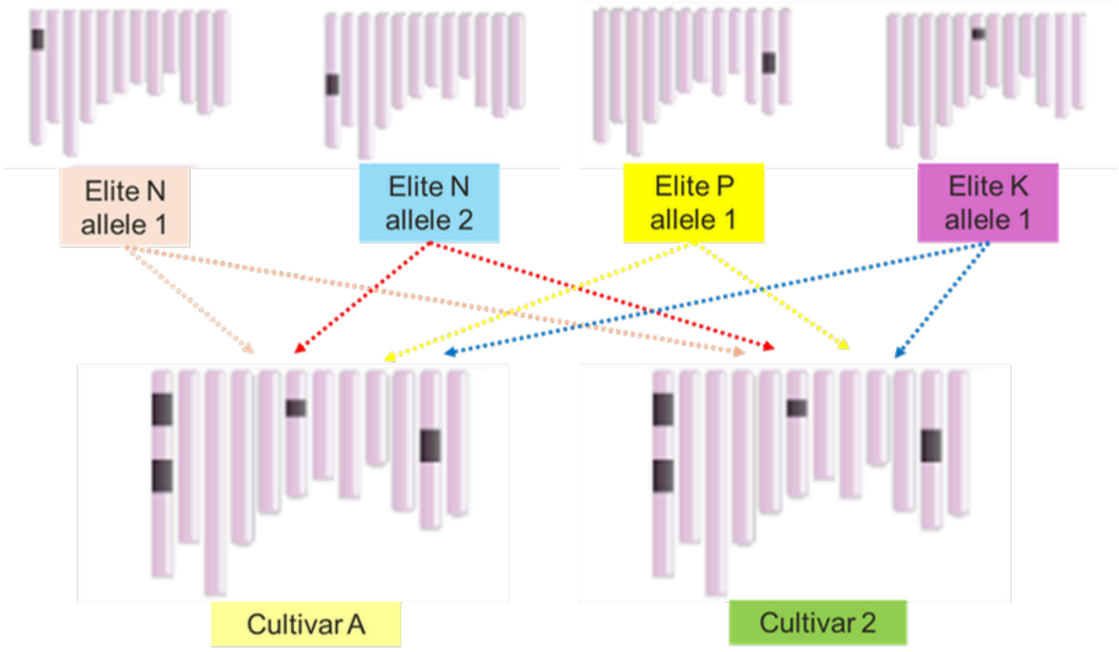
Current research largely focuses on single-nutrient efficiency, such as N or P. But crops often face co-limiting nutrient deficiencies, with different nutrients involving distinct nutrient use efficiency mechanisms. Pyramiding genes - the simultaneous selection for and/or introduction of multiple genes during plant breeding - for N, P, and K efficiency could create cultivars with broad-spectrum nutrient optimization strategies (Fig. 7). To our knowledge, little research has been conducted to date, hence it remains to be seen what the real potential of such strategies will be.

Expanding research beyond rice

While many NUE studies have focused on rice, research should shift their focus towards other major crops, such as wheat, maize, barley, sorghum, oilseeds, legumes, and horticultural crops. Each species has unique nutrient uptake requirements and dynamics, requiring tailored genetic and agronomic solutions. Due to their large genome size, identifying NUE genes in these crops will be challenging but is highly necessary.

Recently, a machine learning pipeline integrating gene regulatory networks and model-to-crop orthology mapping has been reported for accelerating NUE improvement in maize (58). This approach offers a blueprint to systematically enhance NUE in other crops.

Figure 7. *A scheme for pyramiding elite alleles for higher nutrient use efficiency in crops.*



SCIENTIFIC PANEL
ON RESPONSIBLE PLANT NUTRITION

Who needs to do what?

Researchers:

- Design well-targeted product profiles for plant breeding and associated crop trait packages for genetic improvement of NUE, based on good understanding of crop physiology, cropping systems and practices, genotype x environment x management interactions, and market requirements.
- Collaborate with agronomists, soil scientists, crop physiologists, crop modelers, and others throughout all stages of genetic discovery to breeding research (59).
- Use common protocols for phenotyping and field evaluation. Collaborate and openly share experimental details, genetic resources as well as genotyping and phenotyping data.
- Avoid making exaggerated, unvalidated claims.

Governments:

- Adopt science-based policies and regulations that incentivize breeding and adoption of plant varieties developed with modern genetic improvements methods, including gene editing and transgenics (60).
- Provide sufficient and stable funding to support research on gene discovery and characterization and crop improvement for NUE, including advanced phenotyping and field-testing facilities and networks.

Private sector:

- Invest more in R&D on crop genetic improvement of nutrient use efficiency in major crops.

Non-governmental organization and news media:

- Stay up-to-date and open-minded with scientific advancements of genetic improvement strategies for crops, particularly new genetic and breeding technologies.
- Communicate and inform properly and based on science – don't spread misleading information.

SCIENTIFIC PANEL
ON RESPONSIBLE PLANT NUTRITION

What would sucess look like?

1

Genetic approaches are a key component of an integrated, responsible plant nutrition vision (61) for the future. They must be advanced and deployed alongside novel fertilizers (7) and improved nutrient management technologies and practices (6) to achieve significant and lasting improvements in productivity, nutrient use efficiency, as well as environmental and economic benefits.

2

A vision of success is, therefore: within the next 20 years, crop breeding programs will systematically include NUE-related traits as must-have or desirable traits, taking full advantage of genetic discoveries and new breeding techniques and releasing and adopting more nutrient-efficient crop cultivars by farmers worldwide.

SCIENTIFIC PANEL
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