



Nitrogen use efficiency (NUE): elucidated mechanisms, mapped genes and gene networks in maize (*Zea mays* L.)

Shabir H. Wani¹ · Roshni Vijayan² · Mukesh Choudhary³ · Anuj Kumar⁴ ·
Abbu Zaid⁵ · Vishal Singh⁶ · Pardeep Kumar³ · Jeshima Khan Yasin⁷

Received: 31 May 2021 / Revised: 22 November 2021 / Accepted: 7 December 2021 / Published online: 22 December 2021
© Prof. H.S. Srivastava Foundation for Science and Society 2021

Abstract Nitrogen, the vital primary plant growth nutrient at deficit soil conditions, drastically affects the growth and yield of a crop. Over the years, excess use of inorganic nitrogenous fertilizers resulted in pollution, eutrophication and thereby demanding the reduction in the use of chemical fertilizers. Being a C₄ plant with fibrous root system and high NUE, maize can be deployed to be the best candidate for better N uptake and utilization in nitrogen deficient soils. The maize germplasm sources has enormous genetic variation for better nitrogen uptake contributing traits. Adoption of single cross maize hybrids as well as inherent property of high NUE has helped maize cultivars to

achieve the highest growth rate among the cereals during last decade. Further, considering the high cost of nitrogenous fertilizers, adverse effects on soil health and environmental impact, maize improvement demands better utilization of existing genetic variation for NUE via introgression of novel allelic combinations in existing cultivars. Marker assisted breeding efforts need to be supplemented with introgression of genes/QTLs related to NUE in ruling varieties and thereby enhancing the overall productivity of maize in a sustainable manner. To achieve this, we need mapped genes and network of interacting genes and proteins to be elucidated. Identified genes may be used in screening ideal maize genotypes in terms of better physiological functionality exhibiting high NUE. Future genome editing may help in developing lines with increased productivity under low N conditions in an environment of optimum agronomic practices.

✉ Shabir H. Wani
shabirhussainwani@gmail.com;
shabirhwani@skuastkashmir.ac.in

¹ Genetics and Plant Breeding, Mountain Research Centre For Field Crops, Sher-E-Kashmir University of Agricultural Sciences and Technology of Kashmir, Khudwani Anantnag, J&K 192101, India

² Regional Agricultural Research Station-Central Zone, Kerala Agricultural University, MelePattambi, Palakkad, Kerala 679306, India

³ ICAR-Indian Institute of Maize Research, Ludhiana 141001, India

⁴ Centre for Agricultural Bioinformatics (CABin), ICAR-Indian Agricultural Statistics Research Institute, New Delhi 110012, India

⁵ Plant Physiology and Biochemistry Section, Department of Botany, Aligarh Muslim University, Aligarh 202002, India

⁶ Department of Plants, Soils and Climate, Utah State University, 4820 Old Main Hill, Logan, UT 84322, USA

⁷ Division of Genomic Resources, ICAR-National Bureau Plant Genetic Resources, PUSA Campus, New Delhi 110012, India

Keywords Co-expression networks · Maize · NUE · Mapping · Productivity · Quantitative trait loci

Introduction

Maize (*Zea mays* L.) is the world's most important crop in terms of production. Due to its high nutritive value (72% starch, 10% protein, 4.8% oil, 8.5% fiber, 3% sugar and 17% ash), maize is the most multifaceted crop (Ahmad et al. 2018) and an important cereal for human and animal consumption, giving adequate quantity of energy and proteins (Wondesen and Sheleme, 2011). Globally, maize ranks third in cereal production after rice and wheat. Total maize produced over the world covering 170 maize growing countries was 1.15 billion MT which covers the ~ 197 million hectares area in 2020 (FAOSTAT,

2020). Among the 170 countries, four countries, viz., United States, China, Brazil and Argentina together contribute for over 65% of worldwide production while three countries, viz., China, USA and Brazil contribute more than 47% of global area under maize. United States leads maize production with average productivity of 10.5 MT/ha followed by Brazil at 7.9 MT/ha. In developed countries. The average productivity of maize is 6.7 t ha^{-1} while it is 2.4 t ha^{-1} in developing countries (Khalily et al. 2010). In South America, Africa and China, maize is one of the most important food crops (Khalily et al. 2010; Wondesen and Sheleme 2011). Though, India is in the 4th position with 4.6% of total global acreage, it ranks at 7th place with only 2.4% of the global production (FICCI 2021). India lags far behind from the United States in terms of maize production and productivity (Ansari et al. 2015). Among the many reasons for this sub-optimal productivity, one of the major causes is relatively lower adoption of high yielding single cross based long duration hybrids. However, last decade's trend has shown a significant increase in area under single cross hybrids (Yadav et al. 2015).

Global population is increasing at an exponential rate and it is estimated that, by 2050 AD, the world population will be near 9.5 billion (U.S. Bureau of the Census 2009). To feed the burgeoning population, food production must be increased by around 56% without any peril to environmental health (Bloch et al. 2020). During 1960s, Green Revolution made India a self-reliant country for food grains; but, impacted large-scale adoption of high input intensive cropping system. This resulted in over-exploitation of ground water resources at an alarming rate, soil health deterioration from excessive imbalanced fertilizer application, plant protection chemicals and erosion of genetic diversity. Shift towards rice–wheat based monocropping from diversified multiple cropping systems has contributed for deterioration (Choudhury et al. 2013). Crop diversification involving low input-intensive or higher resource-efficient (water and nutrients) cereals like maize in combination with legumes, oilseeds etc. can overcome many of the shortfalls associated with soil and environmental health which surfaced in post-green revolution era (Sood et al. 2009). In north India, maize is grown as successive to rice replacing the existing rice–rice or rice–pulse cropping system due to water scarcity for rice. This is probably the reason for its gaining popularity in conservation agriculture (Kumar et al. 2015).

Adequate use of nitrogen inputs for synchronous improvements in grain yield and nitrogen use efficiency (NUE) has been regarded as a contingent blueprint for development of sustainable agriculture (Wang et al. 2019). Among all the field crops, cereals share the maximum proportion in food security but the supply of optimum nitrogen (N) with 25 to 30% NUE is the new challenge in

cereals (Sheoran et al. 2021). Further, maize being a high yielder has direct impact on food security of a nation. Among cereals, maize has got the highest yield potential, which necessitates more requirements of N and other resources for obtaining higher yields. But providing excessive fertilization brings more harm to the agricultural soils, environment and even for human health (Gou et al. 2010). It leads to pollution of the soil and prevents the optimal utilization of N, or reducing the NUE. Integrated agronomic approaches along with molecular genetic approaches to improve the photosynthetic efficiency are utilized to get better yields of maize without more application of nitrogenous fertilizers, thereby improving the NUE. Recently, very interesting reviews were published on NUE in major crops like cereals (Sandhu et al. 2021) rice (Lee 2021), wheat (Islam et al. 2021) but not maize. Therefore, in the present review, we emphasized the role of N in maize and reviewed its optimum usage for better yields, improved NUE by various agronomic, genetic and molecular breeding approaches in dissecting the NUE contributing factors in maize.

Role of N in maize and its deficiency

Balanced nutrition is an essential requirement in increasing the production and quality of food grains. Among nutrients supplemented by any agronomic practice, N ranks top (Frink et al. 1999). Other than carbon, hydrogen and oxygen, N is the main building block of plant tissues. It makes up to 1–4% of plant's dry matter (Humtsoe et al. 2018) and is a constituent of protein and nucleic acids; hence, its deficiency in soil reduces growth and yield (Haque et al. 2001). N plays a significant role in various physiological processes of plants. N being a component of ATP, amino acids, chlorophyll and nucleic acids plays an important role in energy transfer and metabolic processes contributing to higher production in maize (Wang et al. 2017). N is the major component of photosynthetic organelle, chlorophyll's structure affecting the production of dry matter, leaf area and photosynthetic efficiency (Tafteh and Sepaskhah 2012). In maize, N is deposited in storage proteins such as Zein in the endosperm and Globulin in the embryo of maize, providing nutrition during seed germination (Moose and Below 2009). Maize root system and its branching pattern influence N uptake from soil solution and is assimilated into amino acids (Moose and Below 2009). N uptake from the soil continues till flowering and then declines briefly after flowering. (McCullough et al. 1994; Naeem et al. 2018; Qi et al. 2019; Fernandez et al. 2020). N assimilation occurs through the different pool of carbon acceptors in C_4 photosynthesis mechanism of maize in comparison to C_3 plants (Moose and Below 2009). N is

initially required to support continued growth and high rates of starch synthesis in the endosperm of maize seeds. The most sensitive and highly correlated component trait of maize grain yield in response to N is kernel number (Moose and Below 2009). Growth regulators, particularly cytokinins and polyamines, serve as secondary signals to coordinate the developmental processes (Sakakibara et al. 2006).

Enough supply of N extends leaf area effectively. N delays senescence and plays essential role in initiation of cob and tassel. N stress symptoms appear on lower older leaves. Mid-rib of leaves with V-shaped yellow discoloration coalesces and the entire leaf turns light green (Ding et al. 2005; Clay et al. 2006). Later, these V-shaped regions develop necrotic lesions and then the leaf dries up. Plant vigor is also affected severely. The chlorophyll meter is an instrument used for measuring leaf chlorophyll content (Rostami et al. 2008) and it reflects N deficiency by indirectly indicating a reduction in photosynthetic activities. Deficiency is observed for inadequate N availability (N is lost through denitrification and leaching or run-off). N deficiency causes poor growth and development of maize plants (Sheoran et al. 2021). Further, improper N supply affects the source sink relationship (Torbert et al. 2011). By maintaining the growth of kernel function throughout the grain filling stage, it reflects its significance in both the number of developed kernels and final size of kernel (Hopf et al. 1992; John and Schmitt 2007). N stressed plants exhibit reduced photosynthetic capacity due to degradation of chlorophyll resulting in decreased flow rate of available photosynthates to the growing regions. Leaf expansion and photosynthetic rates of maize are drastically reduced by low N stress (Muchow 1989). Similarly, maize grown in N-stressed soils produced lower grain number and less grain weight (Eck 1984), due to reduction in the number of fertilized ovum, kernel abortion and other changes at physiological and biochemical level that results in substantial reduction of grain yield (Uhart and Andrade 1995). Under N stress, anthesis–silking interval (ASI) increases. Reduction of grain yield per cob may become drastic if the ASI goes beyond five days (Elings et al. 1996). The common effects of N deficiency on maize plants are on relative male and female flowering time (anthesis–silking interval), number of cobs per plant, and number of kernels per ear (Ribaut et al. 2007). The positive relationship between the nutrient supply and seed weight may be due to a higher growth rate of seed during grain filling stage (Khan et al. 2005).

N deficiency adversely affects the growth of maize plant and decreases the shoot to root ratio (Steer and Harrigan 1986), radiation use efficiency, radiation interception, dry matter partitioning, and growth of reproductive organs (Marschner 2012). Plant biomass is drastically reduced and

premature senescence occurs (McConnell et al. 1995), leaves turn pale yellowish green color in the early stage of growth and become more yellow to orange or red in the final stages of growth (Kravchecko et al. 2003). If deficiency exists for a longer time, then the senescence of older leaves occurs. Thus, both the reproductive and vegetative phenological developments are retarded due to N deficiency.

Availability of soil N to the plants and fertilizer application

N is one of the critical components for high productivity and yield and the most important supplement to meet the food demand of increased population (Aseel et al. 2019). N exists as surplus gas in the atmosphere (~ 78%) and soil (2–20 t/ha) (Bockman et al. 1990) but its availability depends on its presence in reduced form i.e. either nitrate or ammonia (Huang et al. 2000). Further, atmospheric N must be fixed in the soil through symbiotic or non-symbiotic bacteria colonizing roots in cereals to be made available to the biological world (Parnell et al. 2016). In soil, N exists both in organic and inorganic forms; of these, organic N contributes 95% of the total N present and the remaining 5% is contributed by inorganic and other forms of N. However, crop easily utilizes the inorganic form since availability of organic N heavily depends on mineralization kinetics of organic matter (oxidation, decomposition and release). Among the N forms available in soil, only the nitrate (NO_3^-) and ammonium (NH_4^+) forms are absorbed by the plant but their availability is limited to only 2% of total N present in the soil (Hailegnaw et al. 2021). The organic form of N cannot be assimilated by the plant and requires mineralization of organic N to inorganic N through amination and ammonification (Rangel and Silva 2007). It has been envisaged that, the total reserve of N in the soil is not equal to N available to the plants (Amado et al. 2002), because mineralized N varies with species, quantity of organic residues, microbes, temperatures, moisture, aeration and humidity (Mary et al. 1996). Parts of mineralized N in soil may be lost, when there is an excess application of N in inorganic form, resulting in ground water contamination, and emission of N-based GHG's, complicating the environmental hazard. The demand for N among crops is much higher than the available soil N reserve (Vitousek and Howarth 1991). Light soils and soils with low organic matter content are usually considered as more prone to N deficiency. Sometimes climatic conditions also cause N deficiency, such as cold weather, especially in the early winters. Excessively wet or leached soil, soil with very high or very low pH, and also fields with fast-growing crops often show N

deficiency. Thus, N present in the soil may be lost by ammonia volatilization, denitrification, leaching, soil erosion and uptake by plants (Silva 2005). In another study, soil acidification in maize stunted the growth and reduced the N uptake and NUE. Pan et al. (2020) reported ~ 24% higher NUE at pH 6.0 compared to pH of 4.0 in clay ultisols soil.

In a cereal crop like maize, N inputs are usually necessary to optimize crop yield, grain quality and profitability over short interval (Ma et al. 2008; Jin et al. 2012). Under the current scenario, the goal of high yield is possible only through the use of chemical nitrogenous fertilizers (Ma et al. 2014). In most of the maize growing regions, irrespective of low marginal return and NUE, N rate is gradually increasing. In 2017, about 109 million tons of N fertilizer was consumed globally for total agricultural production (FAO 2017) and is predicted to reach 443 million tons by 2050 (Sheoran et al. 2021).

NUE reflects the inter-relationship between soil components and plant system (Good and Beatty 2011) or how much per unit economic returns obtained in the form of yield by using per unit fertilizer. However, plants can uptake up to 30–40% of total applied N (Santos et al 2019). Excessive application of N can increase the cost of production because of low NUE due to volatilization losses (Hammad et al. 2017) and nitrate leaching (Hong et al. 2007), at places of intensive agricultural practices (Singh 2005). Only 47% of the total N applied globally in fields, is converted into grains or converts into organic matter; whereas, the remaining is lost in gaseous forms (Sheoran et al. 2021). Due to low NUE, there is an annual economic loss of \$680 million to \$1 billion for Canadian farmers (Biswas and Ma 2016). It is, therefore, worthwhile to improve the NUE and achieve better growth and development through optimum N (Li et al. 2020). Farmers' economic situation is a major limiting factor affecting balanced nutrient applications (Below 2002); and hence, stratified cultivable area based on annual N application to field crops (Sripada et al. 2005).

Fertilizers containing N are applied initially as basal dose and later as split doses due to volatility of most of the nitrogenous compounds. Time of application decides a lot about the availability of N to the plants. For maize, mid-summer is the peak time when the plant uses the most N, so ideally N application should peak during that period. Warm, less-tilled, poorly drained soils pose a problem of N availability due to leaching and denitrification. Though N is abundant in many soils, N deficiency probably continues to be a very serious problem globally.

The effect of externally applied ammonium (NH_4) on plant growth is influenced by the stages of growth and concentration of N in soil. N metabolic pathway enzyme, Glutamate synthetase activity was unaltered when NH_4 was

applied to 3-day-old seedlings. but, upregulated when applied to 18 – 23 days old seedlings. Seedlings stage prolonged N stress reduced the rate of subsequent dry matter accumulation, indicating critical N requirement for maximum NUE. In N metabolic pathway enzymes, higher growth was observed, when applied in a combination of both NO_3 and NH_4 sources of N (Handa et al.1985). In a recent study, suitable fertilizer placement depth (25 cm) increased NUE and maize yield (Wu et al. 2021).

Nitrogen use efficiency in maize

N is one of the most critical inputs that define crop productivity and yield under field conditions. It must be supplemented to meet the food production demands of an ever-increasing population (Aseel et al. 2019). The NUE has been classified as agronomic efficiency (aNUE), physiological efficiency (PhE), agro-physiological efficiency (aPhE), apparent recovery efficiency (ARE), and utilization efficiency (UE) (Santos et al. 2003). aNUE for grain maize has been defined as the increment in grain yield through per unit of applied N (Wang et al. 2019). It is the product of N uptake efficiency (Plant N accumulation/N uptake from the soil) and N utilization efficiency (yield/plant N). The N uptake per unit of N available in the soil is called recovery efficiency. Nitrogen harvest index (NHI) is defined as partitioning of total plant N into the grain (Fageria 2014). NHI appears to be under genetic control, other indices of NUE are observed as largely affected by crop management practices and environmental factors. N uptake efficiency (NUpE) indicates the fraction of N uptake from the total available N from all sources and represents the ability of crops to take up N from soil also called nitrogen recovery efficiency (Burns 2006; Wang et al. 2019; Li et al. 2020). However, nitrogen utilization efficiency (NUtE) or nitrogen internal efficiency indicates how much grain yield produced per unit N-uptake and represents the efficiency with which crops use the absorbed N to grow and give yield (Schenk, 2006, Wang et al. 2019; Li et al. 2020). Improvement in the NUpE leads to low loss of N in soils, on the other hand NUtE leads to high yield in low N inputs (Li et al. 2020), so both NUpE and NUtE may be considered in improving NUE. Thus, the overall NUE can be defined as the harvested yield per unit used of N which is available in the soil (Lassaletta et al. 2016). It is vital to enhance both uptake and utilization efficiency of N-applied to reduce the N losses while meeting the crop N requirements. The N-utilization largely depends on the photosynthetic efficiency of the plants and the subsequent assimilation and translocation process of photosynthates into the economic parts of the plant (mostly grains), (Shewry 2007). The utilization efficiency of applied N may

be enhanced by the selection of genotypes for traits that are helping to produce higher yield with low N application. The more adapted genotypes in low N conditions are the better sustainable strategy to improve NUE (Hire and Lea 2018). NUE is a quantitative trait which is expected to be controlled by many genes.

Higher rates of nitrogenous fertilizer application are considered as the key to high productivity. Higher responsiveness of maize yield for supplemental N, leads to the annual application of ~ 27–63 million tonnes of N in 2050 (Alexandratos and Jelle 2012). This has caused increased pressure on water and soil quality causing degradation of natural soil health. Maize NUE varies from 25 to 50% (Tilman et al. 2002; Aseel et al. 2019) which indicates that half or more of the N applied is lost to the environment (Moose and Below 2009). Another estimate measured the NUE for maize as 33% or less worldwide (Krupnik et al. 2004). So, higher doses of N application reduce the NUE (Pan et al. 2020) and adversely affect the environment by increasing soil acidification, environmental pollution and decrease in soil microbial activity (Chen et al. 2014; Zhu et al. 2016). Based on the previous studies, 1% increase of NUE can save upto US\$ 1.1 billion annually (Kant et al. 2011). Therefore, developing maize genotypes with high NUE can prove to be the best option for increasing the grain yield under low N conditions or minimum N losses and maintaining the health of the environment (Santos et al. 2019).

Studies exhibited the presence of interaction of genotypes with N fertilization and genetic variability for NUE in maize (Bertin and Gallais 2000b, a). At high N input, genetic variation in NUE was said to be due to variation in N uptake, whereas at low N input, NUE variability was due to differences in N utilization efficiency (Gallais and Hirel 2004). Past progress in selecting genotypes for NUE has been limited because of the complexity of the genetic network regulating plant N metabolism (Moose and Below 2009). Much of the research on NUE has been focused on productivity and physiological response of maize genotypes to different N management practices (Giller et al. 2004). NUE in maize is governed by interactions between soil N levels, N availability due to microbial activity in the rhizosphere, and the ability of the maize plant to assimilate and use acquired N for plant growth (Gallais and Coque 2005).

Factors affecting NUE

NUE in the plant can be affected by plant morphological features, N application, time of application, etc. It is important to understand these factors to better understand a complex trait like NUE to develop higher NUE cultivars.

Root system architecture (RSA) regulators

Roots play a significant role in the acquisition of water and mineral nutrients that are essential for plant's survival by affecting yield and production in agriculture (White and Brown 2010). N uptake is strongly influenced by root structure and its functioning, although uptake is limited by sink capacity (Hawkesford 2014). Development and morphology of the root architecture (root/shoot ratio, root size, and root distribution in the soil profile) of the plant are important factors influencing the N uptake from the soil (Eghball et al. 1993). Better N uptake, root growth and development increases the NUE by preventing leaching losses of N fertilizer and inherent soil N resulting in reduced groundwater contamination (Lynch 2013). With the improvement of root structure, there is a significant increase in root dry weight, absorption area and root/shoot ratio for water absorption (Liu et al. 2017). Strong root architecture per unit of leaf area is considered as an index to maintain high photosynthetic rates and duration as well as prolonged stay green leaf character, thus, providing sufficient photosynthates to be deposited in grains to achieve high yields and higher NUE (Kang et al. 1998; Liedgens and Richner 2001). In maize, root system architecture (RSA) is a key determinant of water and nutrient uptake efficiency and is described as the organization of primary root and derived branches (Hochholdinger and Zimmermann 2008). A greater NUE was obtained in a new maize variety with higher root dry weight and root-shoot ratio. A positive correlation was observed between the NUE and root-shoot ratio at the silking stage of crop growth (Yu et al. 2015). Breeding for root traits may improve N uptake efficiency in maize (Coque et al. 2008). Considerable genetic variation for NUE at low N in maize has been reported (Moll et al. 1982) and root morphology has been observed as important in uptake of low mobility nutrients (Nye and Tinker 1977).

Rate and time of N application

The NUE is significantly affected by N rates applied in the soil since a negative relationship between the increase in fertilizer N-rate and NUE exists due to rapid losses of N when the input exceeds the crop assimilation capacity (Meisinger et al. 2008; Zhu et al. 2016). Although, higher doses of N fertilizers increased grain yield, kernel, and cob number significantly, it has been reported that agronomic N efficiency (AEN), N partial factor productivity (PFPN), and NUE of maize in both rainfed and irrigated conditions decreases with increasing fertilizer dose (Jin et al. 2012; Srivastava et al. 2018). Translocation efficiency was also observed to be reduced with high N supplies compared with lower input (Cox et al. 1986). So, the adoption of

improved N management practices in maize production can increase both grain yield and NUE and minimizes N loading of the environment (Halvorson et al. 2010; Ciampitti and Vyn 2011; Ma et al. 2012; Ma and Biswas 2015).

Although, the rate of N-application is location and soil specific, however, in general, grain yields, biomass and shelling percentage of maize crop is increased with increase in N rates (Nunes et al. 1996). Bakht et al. (2006) reported that N application at 200 kg/ha in Peshawar, Pakistan significantly increased the number of leaves plant⁻¹, number of cobs per plant, number of grains per cob, plant height, grain and biological yield. Chlorophyll 'a' content increased by 30%, 43% and 46% and chlorophyll 'a + b' content by 32%, 46% and 52% respectively with the increase in N application rate from 0 to 100 and 200 kg/ha compared to the control plants (0 N kg/ha) (Biswas and Ma 2016). From an experiment on integrated agronomic management practices of summer maize involving differential N-doses (0–300 kg/ha), Liu et al. (2017) reported that for optimum growth of root systems (development and proliferation), application of N @ 184.5 kg ha⁻¹ significantly improved the root architecture (root length density and root dry weight) without any penalty to the grain productivity. Costa et al. (2002), however, reported that greater root length and root surface area were obtained at 127.5 kg N ha⁻¹ compared with either the absence of fertilizer N or at higher N rate of 255 kg N ha⁻¹. Excessive doses of fertilizer N applications are reported to inhibit root growth and development, thus, reducing the ability of roots to absorb nutrients and water, which causes reduction in NUE (Liu et al. 2017; Wang et al. 2000). Many studies suggested that N applications in optimum quantities during mid and late growth stages significantly improves the N uptake, root characters, assimilation, source-sink translocation and final grain development process, thus leading to higher grain yields and harvest index and thus improving NUEs compared to basal application of whole N in one go (Liu et al. 2017; Sun et al. 2017; Zhou et al. 2017).

The split and time of N application are alternatives to increase the efficiency of fertilizers and minimize losses, allowing for synchronization between the applications and the period of high nutrient demand (Yamada et al. 2006). Split N applications, with the highest rate applied at sowing, for the same final amount of fertilizer, resulted in higher grain yield. The rate of 70 kg N ha⁻¹ in topdressing provided the highest maize grain yield compared with the yield obtained with the rates of 40 and 100 kg N ha⁻¹. Increased N at sowing increased the 1000 grain mass, plant height, ear length, grain number per row and grain number per ear (Lana et al. 2013). Demir et al. 2021, observed that application of 186 kg N /ha with fertigation system increased the silage maize yield (99.6 tone/ha).

Plant density

Plant population is one of the factors affecting NUE. In soils with low N availability, NUE of maize fields increases with the increase in planting density (reduction of row spacing from 70 to 52 or 35 cm) (Beriberi et al. 2008). The mechanism that makes the maize plant to absorb more N with narrow row spacing could be better root proliferation and distribution below ground, suppression of weed growth and increase in light interception during critical growth stages (Sharratt and McWilliams 2005). In a study conducted at Northern China plains it was concluded that choosing the optimum plant density combined with appropriate N management could augment grain yields and the NUE in maize. Further increased plant densities with crowding stress decreases the ability of plants to utilize soil N particularly at the post-silking stage, thus higher rates of N fertilizers were required to acquire higher grain yields (Yan et al. 2017).

Improvement in NUE

Both genotype and environment affect nutrient availability but through breeding efforts, improvement in NUE can be achieved. We can hardly control the environment when the plants are to be grown in large fields, but through manipulation of genetic traits we can certainly improve the production level. Apart from enhancing NUE by genetic methods, few cultural practices are associated with the improvement of NUE. The use of nitrification inhibitors which slows down the oxidation of NH₄, and slow and controlled release fertilizers have been used to reduce N leaching (Sitthaphanit et al. 2010). Incorporating straw with a high C:N ratio and minimum tillage can reduce N leaching. The above strategies can be effective in reducing leaching but the extra cost often makes them prohibitive for use by small holders in rain-fed environments. Timing of fertilizer application and split doses is another low-cost strategy to reduce nutrient leaching, so that nutrient supply is synchronized with plant demand (Gehl et al. 2005). Split application of N is one of the methods to improve NUE by the crop while reducing nutrient loss through leaching and volatilization (Tolessa et al. 1994; Muthukumar et al. 2007). It improves the maize grain yield and increases the economic benefit from increased grain yield (Sitthaphanit et al. 2010). Optimum irrigation in maize can also help in obtaining maximum NUE (Li et al. 2019). Crop rotation, the practice of growing a series of dissimilar or different type of crops in the same area in sequenced seasons plays a vital role in improving soil structure and fertility by increasing biomass (Raun and Johnson 1999). Improved soil structure and fertility helps in establishment of better

root system which eventually helps in attaining better NUE by the plant. Source of N in fertilizers also affects NUE. Ammonium (NH₄) source of N is less prone to leaching or denitrification losses.

Importance of root structure for improving NUE in maize: Genomics perspective

Crop production could have been doubled in the past four decades in part through a seven-fold increase in the application of N fertilizers (Hirelet et al. 2007). General effects of N on maize root growth have been studied extensively in various parts of the world. Agricultural production in the twenty-first century is predicted to be more limited because of lower availability and increased cost of water and nutrient resources (Lal 2007). This emphasizes the need to improve the root system so that plants are better able to capture the essential resources more efficiently. Pot experiments with maize have shown that maize roots are thinner and longer in ammonium rich zones (Zhang and Barber 1993).

Quantitative trait loci (QTL) for root traits and NUE

Recent advances in QTL identification have become more important in the NUE enhancement of crop plants including maize. QTL identification and gene mapping is an effective tool to find the key regions of the chromosomes that segregate for NUE (Fig. 1). QTL underlying grain yield and associated traits under normal and low-N stress conditions could hasten the development of NUE varieties in maize (Ertiro et al. 2020). *Root-ABA1*, a major QTL has been mapped for root features and ABA levels in leaf (Giuliani et al. 2005; Landi et al. 2005). Number of aerenchyma cells provides a good indicator of a root growth pattern. With the higher number of aerenchyma cells, the root volume may increase to have better exploration of nutrients in soil. Four QTLs contributing to aerenchyma formation were reported on chromosome 3 (*Qaer3.10*), chromosome 5 (*Qaer5.05–6*), chromosome 9 (*aer9.07–8*) and chromosome 10 (*Qaer10.04*) from maize × teosinte (*Zea luxurians*) crosses. Some QTLs for the traits correlated with NUE and N assimilation have been reported in maize under low N (LN) and high N (HN) conditions (Agrama et al. 1999; Gallais 2001; Hirel et al. 2001; Gallais and Hirel 2004; Ribaut et al. 2007). The brief information of the QTL studies on various traits governing NUE in maize has been provided in Table 1.

The proposed hypothetical ideotype for RSA of maize for higher NUE is, optimal numbers and steeper angles of crown roots which could modulate rooting depth and

subsequently enhance water and N acquisition (Mi et al. 2010; Lynch 2011, 2013; Trachsel et al. 2013; Saengwilai et al. 2014). Maize inbred lines showing high NUE apparently have bigger root diameters than lines with a lesser NUE under low-N conditions (Yang et al. 2019). A thorough understanding of the genetic basis of RSA is the first key step in altering RSA toward better nutrient uptake. QTL mapping has been a major approach in investigating the genetic basis of maize root systems, as root traits are genetically controlled by a number of small-effect loci (deDorlodot et al. 2007; Cai et al. 2012). Significant variation in RSA has been known to exist among maize genotypes, which provides an abundance of genetic material for QTL mapping (Jenison et al. 1981; Landi et al. 1998; Tuberosa et al. 2003; Chun et al. 2005; Kumar et al. 2012). After the first maize RSA QTL reported by Lebreton et al. (1995), varying growth conditions, growth stages and different mapping populations were studied (Hund et al. 2011). However, the localization of these QTLs was inconsistent among the different studies. More QTL analyses for RSA would be required to identify consistent QTL for any future map-based cloning and marker assisted selection.

A low N condition of the soil is a major cause of yield loss in tropical maize coupled with water stress (Pingali and Pandey 2001). Therefore, the efforts for developing cultivars that outperform controls under low N conditions are increasing and a better understanding of the genetic basis of maize development under low N conditions is required to accelerate and improve selection efficiency (Ribaut et al. 2007). Five stable QTLs were identified for low N environments and five co-localized with QTLs identified for ASI or for the number of ears per plant under low N conditions (Ribaut et al. 2007). Mandolina et al. (2018) identified two co-localized QTLs for grain yield, NUE, high biomass and nitrogen harvest index namely *QTL-1* and *QTL-6*. These may be helpful to select for better NUE and high yield simultaneously. Only a few studies have been done to identify QTLs for low-N stress (Gallais and Hirel 2004). Bartin and Gallais (2001) have shown that the QTLs detected at high N input were different from those detected at low N input. Three QTL regions control maize RSA traits, which could be promising candidates for cloning the underlying genes for improving maize root system, as well as water, N and phosphorus use efficiency (Liu et al. 2017). Nitrogen remobilization (NRE) in plants from source to sink organs is an vital phenomenon governed by complex transcriptional regulatory networks (Gong et al. 2020). Two candidate genes namely *ZmASR6* and *GRMZM2G172230* for a major QTL of NRE were identified (Gong et al. 2020), Hormone-coupled transcription factors and downstream target genes disclose a gene regulatory network for the NRE phenomenon after silking

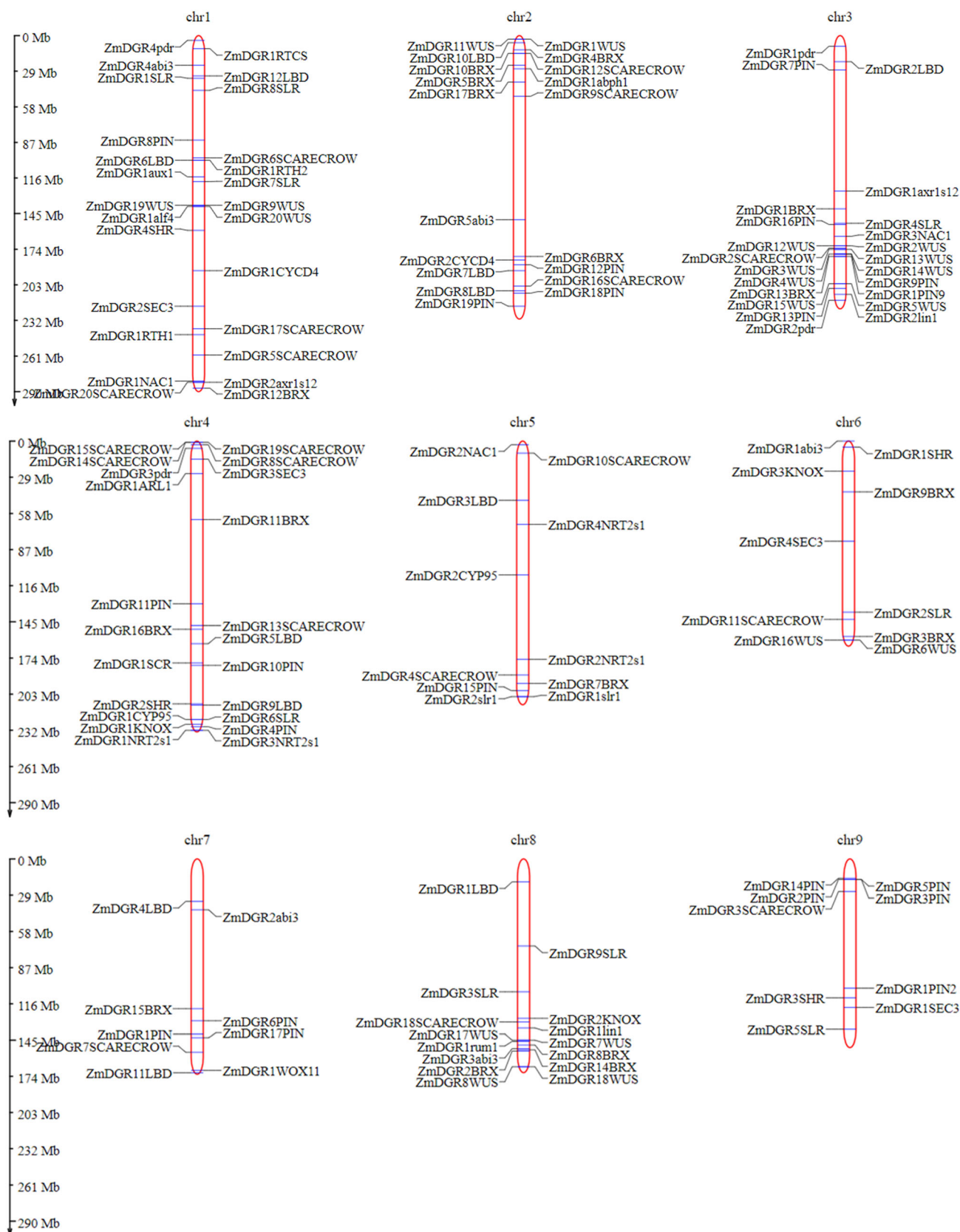


Fig. 1 Physical map of maize with *in silico* predicted positions of identified NUE contributing genes. *In-Silico* gene prediction and mapping tools were used to identify and map the genes (Zm-Zea mays; DGR-markers identified at Division of Genomic Resources, NBPGR, New Delhi)

Table 1 Details of QTL studies on various traits governing the NUE in maize

Parents	Population type & size	Marker type & No.	QTLs	Chr	Phenotypic Variance Explained (R^2 , in %)	Traits	References
B73 × G79	F _{2,3} (214)	RFLP (108)	<i>Bnl9.13</i>	1	15.2	Ear leaf area, Plant height and grain yield/plant under low-N conditions	Agrama et al. (1999)
F2 × Io	RILs (99)	RFLP (152)	42	7 and 9 All except 7 and 10	9.2–13.4	Grain yield/plant under low-N	Hirel et al. 2001
Ac7643S5 × Ac7729/TZSRWS5	F _{2,3} (240)	RFLP	5 (stable)	1	0.5–8.0	Grain yield under N stress	Ribaut et al. (2007)
F2 × Io	RILs (99)	RFLP (152)	24	All except 3, 7 and 10	9–21.9	¹⁵ N abundance	Coque et al. (2006)
F2 × Io	RILs (114)	SSR (167)	608 (72 distinct QTLs clusters)	All	–	Agronomic and physiological traits in normal and N stress	Coque et al. (2008)
Z3 × 87–1	RILs (94)	SSR (260)	17	All except 4 and 9	11–43.7	Root traits	Liu et al. (2012a, b)
Ye478 × B73, Mo17, Qi319, QB80, and ZZ01	BC ₄ F ₂ (413)	SSR (189)	23 (N stress)	2, 3, 4, 5, 6 and 8	4.51–24.27	Grain yield, 100 grain weight, row number per ear and kernel number per row	Liu et al. (2012a, b)
Mo17 × Huangzao4	RILs (239)	–	16 (9 High N + 7 Low N regime)	1,2,3,4,7 and 8	5.4–20.5	Ear leaf length, ear leaf width and ear leaf area	Zheng and Liu (2013)
NUEC2 × NUEC4	DH (60)	SNP (754)	30	All except 1 and 7	17–45	Seedling root traits	Pestsova et al. (2016)
Ye478 × Wu312	RILs (218)	SSR (184)	184	All	4.2–53.6	NUE related traits	Li et al. (2015)
B100 × LP2	RILs (181)	SSR (196)	3	1 and 9	8.4–12.3	NUE	Mandolino et al. (2018)

in maize. These results revealed a classy regulatory machinery for NRE and enabled characterization of treasured genes for genetic improvement of NUE in maize. In maize zinc finger protein *Dof1* (DNA binding with one finger) regulates multiple genes in the metabolic pathways and 54 putative *Dof1* genes are reported in maize (Yanagisawa et al. 2004; Peña et al. 2017). Recently, Ge et al. (2020) identified NIN-like protein 5 (*ZmNLP5*) TF as key gene for regulating maize response to N through altered N signalling and metabolism. A list of cloned genes and transcription factors involved in N metabolism and N uptake and distribution in maize are presented in Table 2 and supplementary table 1.

Transcriptomics in identification of NUE genes in maize

Transcriptome profiling approach has the potential to be used to integrate biological information on metabolic processes, including pathways involved in N uptake, assimilation and remobilization. Since last decade, plant molecular biotechnology, combined with dynamic integrative biological studies increased our knowledge to understand the regulatory mechanisms controlling the primary steps of N assimilation and the subsequent metabolic pathways involved in N supply for secondary metabolic processes (Jiang et al. 2018). Several NUE associated genetic experiments have been conducted in arabidopsis

Table 2 A list of cloned genes and transcription factors involved in N metabolism and nitrogen uptake and distribution in maize

S.No.	Gene symbol	Description	Chr	References
1	<i>ZmGS1</i>	Glutamine synthetase 1	1	Prinsi and Espen (2015)
2	<i>ZmGS2</i>	Glutamine synthetase 2	1	Prinsi and Espen (2015)
3	<i>ZmGS3</i>	Glutamine synthetase 3	9	Martin et al. (2006)
4	<i>ZmGS4</i>	Glutamine synthetase 4	5	Martin et al. (2006)
5	<i>ZmGS5</i>	Glutamine synthetase 5	4	www.ncbi.nlm.nih.gov
6	<i>ZmGS6</i>	Glutamine synthetase 6	1	Li et al. (1993)
7	<i>ZmDof1</i>	DOF1 transcription factor	N/A	Yanagisawa et al. (2004)
8	<i>ZmNRT2.1</i>	High-affinity nitrate transporter 2.1	5	Trevisan et al. (2008)
9	<i>ZmNRT2.2</i>	High-affinity nitrate transporter 2.2	N/A	Pii et al. (2016)
10	<i>ZmNiR</i>	Ferredoxin–nitrite reductase	5	Matsumura et al. (1997)
11	<i>ZmNiR2</i>	Ferredoxin–nitrite reductase 2	4	Zanin et al. 2015
12	<i>ZmNR1</i>	Nitrate reductase 1	4	Shaner and Boyer 1976
13	<i>ZmASN1</i>	Asparagine synthetase 1	9	Balyan et al. (2016);
14	<i>ZmASN2</i>	Asparagine synthetase 2	3	Han et al. (2016);
15	<i>ZmASN3</i>	Asparagine synthetase 3	1	www.ncbi.nlm.nih.gov
16	<i>ZmASN4</i>	Asparagine synthetase 4	9	
17	<i>Zmciptk31</i>	CIPK-like protein 1	1	
18	<i>ZmGPI</i>	Glucose-6-phosphate isomerase	7	
19	<i>ZmNPF1.1</i>	Low affinity nitrate transporter 1.1	3	Fang et al. 2021
20	<i>ZmNPF1.4</i>	Low affinity nitrate transporter 1.4	3	Fang et al. 2021
21	<i>ZmNPF2.1</i>	High affinity nitrate transporter 2.1	1	Santi et al. (2003); Guan et al. (2021); Pii et al. (2016); Ibrahim et al. (2017); Garnett et al. (2013) Balyan et al. (2016)
22	<i>ZmNPF2.2</i>	High affinity nitrate transporter 2.2	1	
23	<i>ZmNPF2.3</i>	High affinity nitrate transporter 2.3	5	
24	<i>ZmNPF3.1</i>	Low affinity nitrate transporter 3.1	9	
25	<i>ZmNPF4.10</i>	Low affinity nitrate transporter 4.10	6	
26	<i>ZmNPF5.8</i>	Low affinity nitrate transporter 5.10	6	
27	<i>ZmNPF5.12</i>	Low affinity nitrate transporter 5.12	1	
28	<i>ZmNPF5.13</i>	Low affinity nitrate transporter 5.13	8	
29	<i>ZmNPF5.14</i>	Low affinity nitrate transporter 5.14	6	
30	<i>ZmNPF6.2</i>	Low affinity nitrate transporter 6.2	3	Wen et al. (2017); Wen and Kaiser (2018); www.ncbi.nlm.nih.gov
31	<i>ZmNPF6.3</i>	Low affinity nitrate transporter 6.3	8	
32	<i>ZmNPF6.4</i>	Low affinity nitrate transporter 6.4	10	
33	<i>ZmNPF6.5</i>	Low affinity nitrate transporter 6.5	1	
34	<i>ZmNPF6.6</i>	Low affinity nitrate transporter 6.6	1	
35	<i>ZmNPF6.7</i>	Low affinity nitrate transporter 6.7	5	
36	<i>ZmNPF6.8</i>	Low affinity nitrate transporter 6.8	5	
37	<i>ZmNPF7.4</i>	Low affinity nitrate transporter 7.4	7	Dechorgnat et al. (2019); Oosten et al. (2019); Balyan et al. (2016); www.ncbi.nlm.nih.gov ; www.uniprot.org

Table 2 continued

S.No.	Gene symbol	Description	Chr	References
38	<i>ZmNPF7.9</i>	Low affinity nitrate transporter 7.9	5	
39	<i>ZmNPF7.10</i>	Low affinity nitrate transporter 7.10	4	
34	<i>ZmNPF7.12</i>	Low affinity nitrate transporter 7.12	8	
35	<i>ZmNPF8.1</i>	Low affinity nitrate transporter 8.1	3	
36	<i>ZmNPF8.2</i>	Low affinity nitrate transporter 8.2	1	
37	<i>ZmNPF8.8</i>	Low affinity nitrate transporter 8.8	1	
38	<i>ZmNPF8.9</i>	Low affinity nitrate transporter 8.9	1	
39	<i>ZmNPF8.12</i>	Low affinity nitrate transporter 8.12	7	
40	<i>ZmNPF8.13</i>	Low affinity nitrate transporter 8.13	1	
41	<i>ZmNPF8.14</i>	Low affinity nitrate transporter 8.14	1	
42	<i>ZmNPF8.15</i>	Low affinity nitrate transporter 8.15	1	

(Wang et al. 2003; Gutiérrez et al. 2007) and in other major cereal crops including rice (Kumari et al. 2021), wheat (Peña et al. 2017) and maize (Sekhon et al. 2011; Gong et al. 2020).

Since last decade, transcriptomics approach has been widely applied to identify N-associated candidate genes and to functionally characterize responses to N availability in soil. N-responsive genes have been classified in several classes based on their characteristics. In arabidopsis, a set of NUE associated genes have been identified using microarray studies including known nitrate-induced genes (NR genes), the nitrate transporter (NRT1), glutamine synthetase (GS) and additionally many other novel genes differentially expressed under low- and high-N conditions in soil (Wang et al. 2000; 2003; Gutiérrez et al. 2007). An increasing number of whole genome transcriptome analyses allow us to conduct NUE based analysis in maize (Sekhon et al. 2011; Amiour et al. 2012; Downs et al. 2013; Humbert et al. 2013; Zamboni et al. 2014; He et al. 2020; Gong et al. 2020). In recent study Kumari et al. (2021) identified a total of 62 NUE candidate genes for NUE related traits and their expression in rice.

In maize, a core set of NUE associated genes have been identified in different maize lines by using transcriptomic approaches with different methods (Yang et al. 2010; Schlüter et al. 2012). Predicted initial results of these studies reflected that various genes were associated to alteration in N conditions, but their level of response appeared to be largely dependent on the genotype. These genes may play an important role in wide range of developmental, metabolic and regulatory functions, including transcription factors which are responsible for coordinating multiple genes in a potential regulatory network. Interestingly, a cluster of NUE associated genes could be utilized as biomarkers for both breeding and optimizing fertilizer

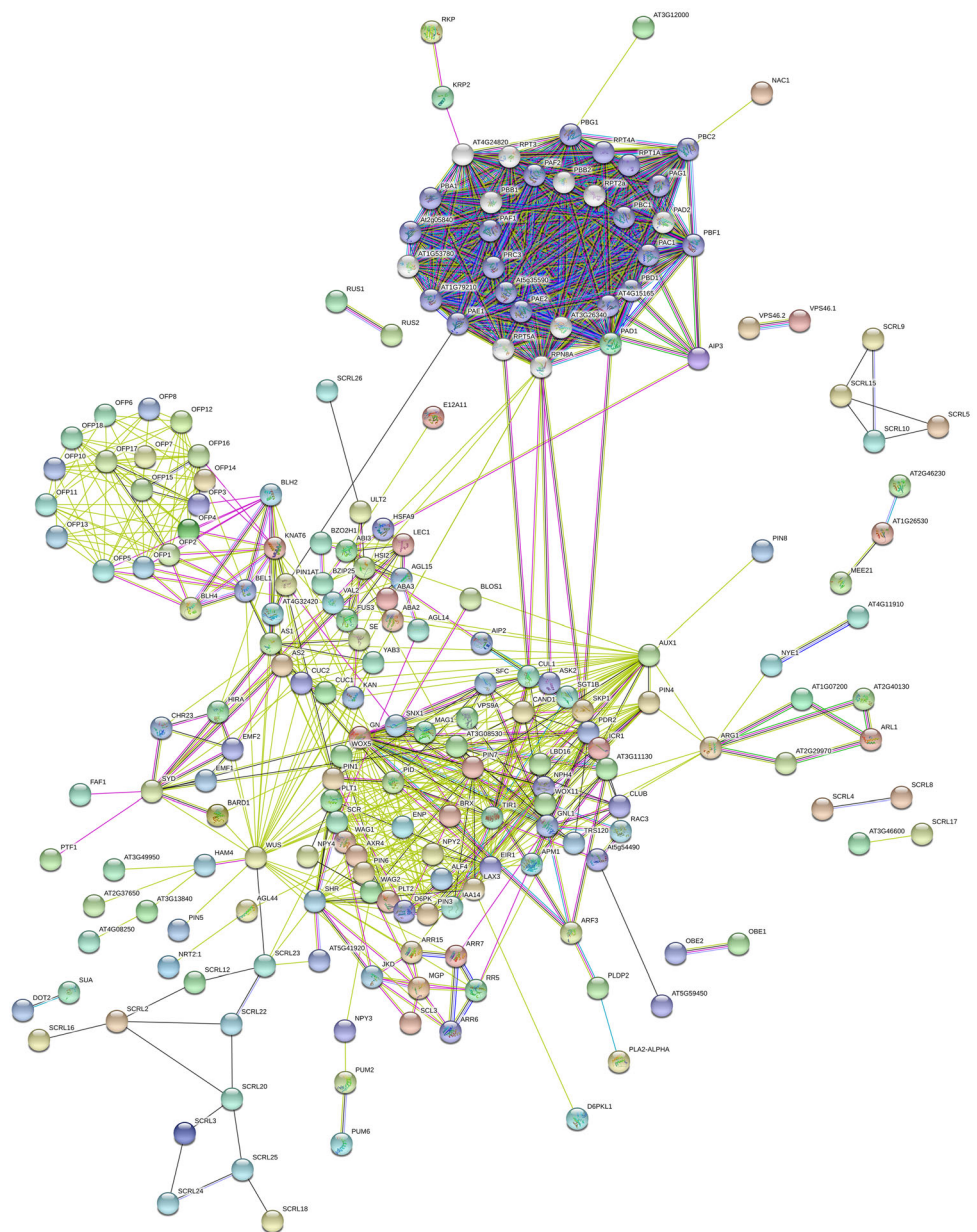
usage (Yang et al. 2010). Methods for identifying target genes from transcriptomic profiling data are part of important approaches towards providing a general framework for computational modeling of inferred networks. In a recent study, to elucidate the genetic basis of NUE related traits by genome wide association study, an association panel of 139 maize inbred lines was genotyped with 50,790 single nucleotide polymorphism (SNP) (He et al. 2020). They reported *Zm00001d025831* and *Zm00001d004633* encoded ammonium transporter1 and transmembrane amino acid transporter family protein as possible significant candidate genes for NUE.

Expression network of genes involved in root architecture and NUE

A network of 113 proteins involved either directly or indirectly in creating an environment to influence the NUE positively and negatively has been identified through system biology approach using co-expression data available in data bases (STRING v11, Szklarczyk et al. 2019) of identified genes depicted in figure (Fig. 2). The major cluster depicted in identified network (Fig. 2) includes SCR, WUS, PIN, NPY family proteins, AGC kinases and AUX1. SHORTROOT and SCARECROW are root patterning genes contributing for its development and overall structure. Apart from these two genes, activity of auxin responsive DR5 promoter with expression of AUX1 (auxin influx carrier protein) and PIN proteins regulates the auxin movement and leads to lateral root development (Malamy 2005).

A minor cluster of 17 OFP transcription factor was found to be linked with BLH2, BLH4, KNAT6, BEL1 and PIN1AT indirectly. This cluster of meristematic functions

Fig. 2 : Network of co-expressing genes contributing Nitrogen Use Efficiency. Co-expression based interaction of genes were plotted to identify key nodes of interaction and putative gene candidates for future genome editing



regulating proteins depicts their role in root branching and root hair developments. WUS, another transcription factor connects all three clusters mentioned above with other proteins like PIN5, HAM4, and BRCA1 which specifically binds to H3K4me3 WUS to repress transcription by chromatin remodeling (STRING database). NTR2 interacts with AGL44, a MADS box transcription factor which is required for nitrate response by root plasticity and together promotes lateral root growth with co-expression of AXR4, an auxin influx facilitator and co-localized with AUX1. This shows that that NRT2.1 nitrate transporter acts as a sensor via regulation of auxin transport.

N-responsive intergenic and intronic long non-coding RNAs

Long non-coding RNAs (*lncRNAs*) are a class of non-coding RNAs longer than 200 nucleotides. They act as source of *phasiRNAs* and sponges for miRNAs; termed as *ceRNA* in many cases as they compete with coding sequences in regulating gene expression. *lncRNAs* play critical role in regulating diverse biological processes, such as transcriptional regulation, dosage compensation and genomic imprinting (Muers 2011; Guil and Esteller 2012; Mercer and Mattick 2013; Fatica and Bozzoni 2014). Although, much information about biological functions of *lncRNAs* in plants is not available so far with recent

advances in rapid development of high-throughput sequencing technologies, large numbers of *lncRNAs* have been identified and functionally characterized in arabidopsis, maize, rice and other plant species using *in-silico* and experimental approaches (Yan et al. 2017). In maize genome, 1802 potential *lncRNAs* have been identified from 18,668 full-length cDNA sequences using bioinformatics tools (Boerner and McGinnis, 2012). In another study, Li et al. (2015) identified 20,163 putative *lncRNAs* and 1704 high-confidence *lncRNAs* by using expressed sequence tag (EST) databases and RNA-seq datasets from 30 different experiments. Recent studies explored the regulation of *lncRNA* expression in response to abiotic stresses in higher plants (Contreras-Cubas et al. 2012; Liu et al. 2012a, b; Matsui et al. 2013; Qi et al. 2013; Wang et al. 2014). Differentially expressed 245 poly (A) + and 58 poly (A)–*lncRNAs* under various stress stimuli have been identified from RNA-seq of arabidopsis seedlings (Di et al. 2014). In maize, Lv et al. (2016) evaluated the potential role of *lncRNAs* with/without polyA tails in response to N resources. Ultra-deep total RNA sequencing was performed to identify the intergenic/intronic *lncRNAs* genes expressed in maize leaves. Among the 7245 identified novel *lncRNAs*, 637 were N-responsive. Through this study, it has been demonstrated that, the predicted *lncRNAs* play a key role in metabolic processes associated with energy, oxidative phosphorylation, and phosphorus and N compounds.

Further annotation of *lncRNAs* in cereal genomes may provide a unique opportunity to understand the molecular mechanism of NUE. Some experimental approaches like overexpression, RNAi and promoter analysis may be utilized to characterize biological functions of *lncRNAs*, which could be important to provide valuable information for NUE leading to maize crop improvement.

Conclusion and future perspectives

NUE is a complex trait, derived from the amalgam of physiological traits. Hence the genetic dissection of N uptake, N flow and N utilization process at cellular, organ, and plant levels needs to be explored through targeting selection for multiple traits, especially root traits. However, such studies are complicated by factors like N regimes, genotypes and developmental stage. Therefore, there is need to explore the root system architecture under different soil types and N regimes using different cultivars. Hence, agronomy targeted breeding can be explored to achieve better genetic gains particularly by targeting efficient accumulation of N in the grain. Furthermore, the integration of association mapping, genomic prediction and ‘omics’ approaches with the phenomic approaches can

contribute significantly in improving NUE in maize. The most challenging task in NUE studies is the precise phenotyping of the traits. The advances in phenomics have enabled to utilise the hyperspectral imaging based field observations (through spectrometers or aerial imagery) as well as automated mobile and fixed platforms (Knyazikhin et al. 2013; Virlet et al. 2017). Considering the generation of enormous datasets (big data), integration of ‘omics’ approaches data into modelling and selection will be the biggest target for plant breeders (Langridge and Fleury 2011). Further, the metabolomics also need to be integrated to interpret the functional characterization of the expression gene networks. The genetic dissection of gene networks can help to apply the metabolic engineering for developing NUE efficient cultivars (Toubiana et al. 2013). In addition, the transgenic breeding should emphasize on the identification of the genes that instead of overexpression can negatively regulate the NUE and hence facilitate the engineering of NUE through genome editing (Wan et al. 2017). Further the breeding of maize for biological N fixation is although a challenging but promising task to improve the NUE (Sheoran et al. 2021). The pan-genomics approach can also be explored to identify unique genes for NUE in maize. Hence, considering the availability of enormous variability, omics and engineering approaches, there lies great opportunities to develop the NUE efficient ideotypes in maize and hence safeguarding the food security and sustainability of nature.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12298-021-01113-z>.

Acknowledgements Authors are grateful to their respective institutions.

Author Contribution SHW conceived the idea, SHW, RV, MK, AK, AZ, VS, PK and JKY wrote the MS.

Funding This work was partially supported by the Indian Council of Agricultural Research –National Bureau of Plant Genetic Resources [PGR/DFP-BUR-DEL-01.01]. AZ is thankful to Aligarh Muslim University and UGC-New Delhi India for financial assistance.

Declarations

Conflict of interest Authors declare that they have no conflict of interest.

References

- Agrama HAS, Zakaria AG, Said FB, Tuinstra M (1999) Identification of quantitative trait loci for nitrogen use efficiency in maize. *Mol Breeding* 5:187–195
- Alexandratos N, Jelle B (2012) World agriculture towards 2030/2050: The 2012 revision

- Amiour N, Imbaud S, Clement G, Agier N, Zivy M, Valot B, Balliau T, Armengaud P, Quillere I, Canas T et al (2012) The use of metabolomics integrated with transcriptomic and proteomic studies for identifying key steps involved in the control of nitrogen metabolism in crops such as maize. *J Exp Bot* 63:5017–5033
- Ansari MA, Prakash N, Ashok Kumar, Jat SL, Baishya LK, Sharma SK, Bungbungcha CH, Sanatombi KH, Sanjay Singh S. (2015). Maize production technology highlighted in North East India. Training Manual RCM (TM)—05. ICAR Research Complex for NEH Region, Manipur Centre, Lamphelpat, Imphal795004
- Aseel DG, Mostafa Y, Riad SA, Hafez EE (2019) Improvement of nitrogen use efficiency in maize using molecular and physiological approaches. *Symbiosis* 78(3):263–274
- Balyan HS, Gahlaut V, Kumar A, Jaiswal V, Dhariwal R, Tyagi S, Agarwal P, Kumari S, Gupta PK (2016) Nitrogen and phosphorus use efficiencies in wheat: physiology, phenotyping, genetics, and breeding. *Plant Breed Rev* 40:167–214
- Bertin P, Gallais A (2000a) Genetic variation for nitrogen use efficiency in a set of recombinant maize inbred lines. I. Agrophysiological results. *Maydica* 45:53–66
- Bertin P, Gallais A (2000b) Physiological and genetic basis of nitrogen use efficiency in maize. I. Agrophysiological Results. *Maydica* 45:53–66
- Bertin P, Gallais A (2001) Physiological and genetic basis of nitrogen use efficiency in maize. II. QTL Detection and Coincidences. *Maydica* 46:53–68
- Bloch SE, Ryu M, Ozaydin B, Broglie R (2020) Harnessing atmospheric nitrogen for cereal crop production. *Curr Opin Biotech* 62:181–188
- Cai H, Chen F, Mi G, Zhang F, Maurer HP, Liu W et al (2012) Mapping QTLs for root system architecture of maize (*Zea mays* L.) in the field at different developmental stages. *Theor Appl Genet* 125:1313–1324. <https://doi.org/10.1007/s00122-012-1915-6>
- Chun L, Mi GH, Li JS, Chen FJ, Zhang FS (2005) Genetic analysis of maize root characteristics in response to low nitrogen stress. *Plant Soil* 276:369–382. <https://doi.org/10.1007/s11104-005-5876-2>
- Clay DE, Ki-In Kim J, Chang SAC, Dalsted K (2006) Characterizing Water and Nitrogen Stress in Corn Using Remote Sensing. *Agron J* 98:579–587
- Contreras-Cubas C, Palomar M, Arteaga-V A, Zquez M, Reyes JEL, Covarrubias AA (2012) Non-coding RNAs in the plant response to abiotic stress. *Planta* 236:943–958. <https://doi.org/10.1007/s00425-012-1693-z>
- Coque M, Bertin P, Hirel B, Gallais A (2006) Genetic variation and QTLs for 15N natural abundance in a set of maize recombinant inbred lines. *Field Crop Res* 97(2–3):310–321
- Coque M, Martin A, Veyrieras JB, Hirel B, Gallais A (2008) Genetic variation for N-remobilization and postsilking N-uptake in a set of maize recombinant inbred lines. 3. QTL detection and coincidences. *Theor Appl Genet* 117(5):729–747
- Costa C, Dwyer LM, Zhou X, Dutilleul P, Hamel C, Reid LM, Smith DL (2002) Root morphology of contrasting maize genotypes. *Agron J* 94:96–105
- Dechorgnat J, Francis KL, Dhugga KS, Rafalski JA, Tyerman SD, Kaiser BN (2019) Tissue and nitrogen-linked expression profiles of ammonium and nitrate transporters in maize. *BMC Plant Biol* 19:206
- deDorlodot S, Forster B, Pages L, Price A, Tuberosa R, Draye X (2007) Root system architecture: opportunities and constraints for genetic improvement of crops. *Trends Plant Sci* 12:474–481. <https://doi.org/10.1016/j.tplants.2007.08.012>
- Di C, Yuan J, Wu Y, Li J, Lin H, Hu L, Zhang T, Qi Y, Gerstein MB, Guo Y et al (2014) Characterization of stress-responsive lncRNAs in *Arabidopsis thaliana* by integrating expression, epigenetic and structural features. *Plant J* 80:848–861. <https://doi.org/10.1111/tpj.12679>
- Ding L, Wang KJ, Jiang GM, Biswas DK, Xu H, Li LF, Li YH (2005) Effects of nitrogen deficiency on photosynthetic traits of maize hybrids released in different years. *Ann Bot* 96:925–930
- Downs GS, Bi YM, Colasanti J, Wu WQ, Chen X, Zhu T, Rothstein SJ, Lukens LN (2013) A developmental transcriptional network for maize defines coexpression modules. *Plant Physiol* 161:1830–1843
- Eck HV (1984) Irrigation corn yield responses to nitrogen and water. *Agron J* 76:421–428
- Elings A, White J, Edmeades GO (1996) Modelling tropical maize under drought and low N. Annual Abstracts. Agronomy Meeting. American Society of Agronomy. Indianapolis, Indiana. November 3–8. p 109
- Fageria NK (2014) Nitrogen harvest index and its association with crop yields. *J Plant Nutr* 37:795–810
- FAO (Food and Agricultural Organization) (2017). <http://www.fao.org/faost at/en/#data/RFN>. Accessed 25 April 2020
- FAO (2020). FAOSTAT data. Food and Agricultural Organization, Italy, Rome. <http://faostat.fao.org/>
- Fang XZ, Fang SQ, Ye ZQ, Liu D, Zhao KL, Jin CW (2021) NRT1.1 Dual-affinity nitrate transport/signalling and its roles in plant abiotic stress resistance. *Front Plant Sci* 12:715694
- Fatica A, Bozzoni I (2014) Long non-coding RNAs: new players in cell differentiation and development. *Nat Rev Genet* 15:7–21. <https://doi.org/10.1038/nrg3606>
- Fernandez JA, DeBruin J, Messina CD, Ciampitti IA (2020) Late-season nitrogen fertilization on maize yield: a meta-analysis. *Field Crops Res* 247:107586
- FICCI (2021) Boosting Growth of India's Maize Ecosystem-Key Imperatives. pp. 9
- Gallais A, Hirel B (2004) An approach to the nitrogen use efficiency in maize. *J Exp Bot* 55(396):295–306
- Gallais A, Coque M (2005) Genetic variation and selection for nitrogen use efficiency in maize: a synthesis. *Maydica* 50:531–537
- Garnett T, Conn V, Plett D, Conn S, Zanghellini J, Mackenzie N, Enju A, Francis K, Holtham L, Roessner U, Boughton B, Bacic A, Shirley N, Rafalski A, Dhugga K, Tester M, Kaiser BN (2013) The response of the maize nitrate transport system to nitrogen demand and supply across the lifecycle. *N Phytol* 198:82–94. <https://doi.org/10.1111/nph.12166>
- Ge M, Wang Y, Liu Y, Jiang LU, He B, Ning L, Du H, Lv Y, Zhou L, Lin F, Zhang T (2020) The NIN-like protein 5 (ZmNLP5) transcription factor is involved in modulating the nitrogen response in maize. *Plant J* 102(2):353–368
- Giller KE, Chalk P, Dobermann A, Hammond L, Heffer P, Ladha JK, Nyamudeza P, Maene L, Ssali H, Freney J (2004) Emerging technologies to increase the efficiency of use of fertilizer nitrogen. In: Mosier AR, Syers KJ, Freney JR (eds) Agriculture and the nitrogen cycle: assessing the impacts of fertilizer use on food production and the environment. Island Press, Washington, pp 35–51
- Giuliani S, Sanguineti MC, Tuberosa R, Bellotti M, Salvi S, Landi P (2005) Root-ABA1, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes. *J Exp Bot* 56(422):3061–3070
- Gong X, Liu X, Pan Q, Mi G, Chen F, Yuan L (2020) Combined physiological, transcriptome, and genetic analysis reveals a molecular network of nitrogen remobilization in maize. *J Exp Bot* 71(16):5061–5073
- Guil SON, Esteller M (2012) Cis-acting noncoding RNAs: friends and foes. *Nat StructMol Biol* 19:1068–1075. <https://doi.org/10.1038/nsmb.2428>

- Guan M, Chen M, Cao Z (2021) NRT2.1, a major contributor to cadmium uptake controlled by high-affinity nitrate transporters. *Ecotoxicol Environ Saf* 218:11226
- Gutiérrez RA, Lejay LV, Dean A, Chiaromonte F, Shasha DE, Coruzzi GM (2007) Qualitative network models and genome-wide expression data define carbon/nitrogen-responsive molecular machines in *Arabidopsis*. *Genome Biol* 8:R7
- Hailegnaw NS, Mercl F, Kulhánek M, Száková J, Tlustoš P (2021) Co-application of high temperature biochar with 3, 4-dimethylpyrazole-phosphate treated ammonium sulphate improves nitrogen use efficiency in maize. *Sci Rep* 11(1):1–13
- Hammad HM, Farhad W, Abbas F, Fahad S, Saeed S, Nasim W, Bakhat HF (2017) Maize plant nitrogen uptake dynamics at limited irrigation water and nitrogen. *Environ Sci Pollut Res* 24(3):2549–2557
- Han M, Wong J, Su T, Beatty PH, Good AG (2016) Identification of nitrogen use efficiency genes in barley: searching for QTLs controlling complex physiological traits. *Front Plant Sci* 7:1587. <https://doi.org/10.3389/fpls.2016.01587>
- He K, Xu S, Zhang X, Li Y, Chang L, Wang Y, Shi Y, Cui T, Dong Y, Lan T, Liu X (2020) Mining of candidate genes for nitrogen use efficiency in maize based on genome-wide association study. *Mol Breeding* 40(9):1–7
- Hirel B, Bertin P, Quilleré I, Bourdoncle W, Atgnant C, Dellay C, Gallais A (2001) Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. *Plant Physiol* 125(3):1258–1270
- 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* 58:2369–2387
- Hochholdinger F, Zimmermann R (2008) Conserved and diverse mechanisms in root development. *Curr Opin Plant Biol* 11:70–74. <https://doi.org/10.1016/j.pbi.2007.10.002>
- Hopf N, Plesofsky-Vig N, Brambl R (1992) The heat shock response of pollen and other tissues of maize. *Plant Mol Biol* 19:623–630. <https://doi.org/10.1007/BF00026788>
- Huang YZ, Feng Z, Fuzhu Z (2000) Study on loss of nitrogen fertilizer from agricultural fields and countermeasure. *J Grad Sch Academia Sinica* 17(2):49–58
- Humbert S, Subedi S, Cohn J, Zeng B, Bi YM, Chen X, Zhu T, McNicholas PD, Rothstein SJ (2013) Genome-wide expression profiling of maize in response to individual and combined water and nitrogen stresses. *BMC Genom* 14:3
- Humtsoe BM, Dawson J, Rajana P (2018) Effect of nitrogen, boron and zinc as basal and foliar application on growth and yield of maize (*Zea mays* L.). *J Pharmacogn Phytochem* 7(6):01–04
- Hund A, Reimer R, Messmer R (2011) A consensus map of QTLs controlling the root length of maize. *Plant Soil* 344:143–158. <https://doi.org/10.1007/s11104-011-0735-9>
- Ibrahim A, Jin XL, Zhang YB, Cruz J, Vichyavichien P, Esiobu N, Zhang XH (2017) Tobacco plants expressing the maize nitrate transporter ZmNrt2.1 exhibit altered responses of growth and gene expression to nitrate and calcium. *Bot Stud* 58:51
- Islam, S., Zhang, J., Zhao, Y., She, M., and Ma, W. (2021). Genetic regulation of the traits contributing to wheat nitrogen use efficiency. *Plant Sci*. 303:110759.
- Jenison JR, Shank DB, Penny LH (1981) Root characteristics of 44 maize inbreds evaluated in 4 environments. *Crop Sci* 21:233–237
- John GW, Schmitt MA (2007) Advisability of fall-applying nitrogen. In: Proceedings of the 2008 Wisconsin Fertilizer, Aglime and Pest Management Conference, held on the 15–17th January, 2008 at University of Wisconsin, Madison, WI. pp. 90–96
- Kant S, Bi YM, Rothstein SJ (2011) Understanding plant response to nitrogen limitation for the improvement of crop nitrogen use efficiency. *J Exp Bot* 62(4):1499–1509
- Khan A, Jan A, Bashir S, Noor M (2005) Effect of nitrogen and seed size on maize crop. I: Stand and plant height. *J Agric Soc Sci* 1(4):380–381
- 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 Nat Acad Sci USA* 110:E185–E192
- Kumar B, Abdel-Ghani AH, Reyes-Matamoros J, Hochholdinger F, Luebberstedt T (2012) Genotypic variation for root architecture traits in seedlings of maize (*Zea mays* L.) inbred lines. *Plant Breed* 131:465–478. <https://doi.org/10.1111/j.1439-0523.2012.01980.x>
- Kumar V, Singh AK, Jat SL, Parihar CM, Pooniya V, Singh B, Sharma S (2015) Precision nutrient and conservation agriculture practices for enhancing productivity, profitability, nutrient-use efficiencies and soil nutrient status of maize (*Zea mays*) hybrids. *Indian J Agric Sci* 85(7):926–930
- Kumari S, Sharma N, Raghuram N (2021) Meta-analysis of yield-related and N-responsive genes reveals chromosomal hotspots, key processes and candidate genes for nitrogen-use efficiency in rice. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2021.627955>
- Lal R (2007) Anthropogenic influences on world soils and implications to global food security. *Adv Agron* 93:69–93
- Landi P, Albrecht B, Giuliani MM, Sanguineti MC (1998) Seedling characteristics in hydroponic culture and field performance of maize genotypes with different resistance to root lodging. *Maydica* 43:111–116
- Landi P, Sanguineti MC, Salvi S, Giuliani S, Bellotti M, Maccaferri M, Conti S, Tuberosa R (2005) Validation and characterization of a major QTL affecting leaf ABA concentration in maize. *Mol Breeding* 15(3):291–303
- Langridge P, Fleury D (2011) Making the most of ‘omics’ for crop breeding. *Trends Biotechnol* 29:33–40
- Lassaletta L, Billen G, Garnier J, Bouwman L, Velazquez E, Mueller ND, Gerber JS (2016) Nitrogen use in the global food system: past trends and future trajectories of agronomic performance, pollution, trade, and dietary demand. *Environ Res Lett* 11:095007
- Lebreton C, Lazicjancic V, Steed A, Pekic S, Quarrie SA (1995) Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. *J Exp Bot* 46:853–865. <https://doi.org/10.1093/jxb/46.7.853>
- Lee S (2021) Recent Advances on Nitrogen Use Efficiency in Rice. *Agronomy* 11(4):753
- Li MG, Villemur R, Hussey PJ, Silflow CD, Gantt JS, Snustad DP (1993) Differential expression of six glutamine synthetase genes in *Zea mays*. *Plant Mol Biol* 23:401–407
- Li M, Xu J, Gao Z, Tian H, Gao Y, Kariman K (2020) Genetically modified crops are superior in their nitrogen use efficiency-A meta-analysis of three major cereals. *Sci Rep* 10(1):1–9
- Li P, Chen F, Cai H, Liu J, Pan Q, Liu Z, Gu R, Mi G, Zhang F, Yuan L (2015) A genetic relationship between nitrogen use efficiency and seedling root traits in maize as revealed by QTL analysis. *J Exp Bot* 66(11):3175–3188
- Li Y, Li Z, Cui S, Chang SX, Jia C, Zhang Q (2019) A global synthesis of the effect of water and nitrogen input on maize (*Zea mays*) yield, water productivity and nitrogen use efficiency. *Agric For Meteorol* 268:136–145
- Liu J, Jung C, Xu J, Wang H, Deng S, Bernad L, Arenas-Huertero C, Chua NH (2012a) Genome-wide analysis uncovers regulation of long intergenic noncoding RNAs in *Arabidopsis*. *Plant Cell* 24:4333–4345. <https://doi.org/10.1105/tpc.112.102855>

- Liu R, Zhang H, Zhao P, Zhang Z, Liang W, Tian Z, Zheng Y (2012b) Mining of candidate maize genes for nitrogen use efficiency by integrating gene expression and QTL data. *Plant Mol Biol Rep* 30(2):297–308
- Liu Z, Gao K, Shan S, Gu R, Wang Z, Craft EJ, Mi G, Yuan L, Chen F (2017) Comparative Analysis of Root Traits and the Associated QTLs for Maize Seedlings Grown in Paper Roll, Hydroponics and Vermiculite Culture System. *Front Plant Sci* 8:436. <https://doi.org/10.3389/fpls.2017.00436>
- Lv Y, Liang Z, Ge M, Qi W, Zhang T, Lin F, Peng Z, Zhao H (2016) Genome-wide identification and functional prediction of nitrogen-responsive intergenic and intronic long non-coding RNAs in maize (*Zea mays* L.). *BMC Genomics* 17:350. <https://doi.org/10.1186/s12864-016-2650-1>
- Lynch JP (2011) Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. *Plant Physiol* 156:1041–1049. <https://doi.org/10.1104/pp.111.175414>
- Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Ann Bot* 112:347–357. <https://doi.org/10.1093/aob/mcs293>
- Mandolino CI, D'Andrea KE, Olmos SE, Otegui ME, Eyh rabide GH (2018) Maize nitrogen use efficiency: QTL mapping in a US Dent x Argentine-Caribbean flint RILs population. *Maydica* 63(1):17
- Martin A, Lee J, Kichey T, Gerentes D et al (2006) Two cytosolic glutamine synthetase isoforms of maize are specifically involved in the control of grain production. *Plant Cell* 18:3252–3274
- Matsui A, Nguyen AH, Nakaminami K, Seki M (2013) Arabidopsis non-coding RNA regulation in abiotic stress responses. *Int J Mol Sci* 14:22642–22654. <https://doi.org/10.3390/ijms141122642>
- Matsumura T, Sakakibara H, Nakano R, Kimata Y, Sugiyama T, Hase T (1997) A nitrate-inducible ferredoxin in maize roots. Genomic organization and differential expression of two nonphotosynthetic ferredoxin isoproteins. *Plant Physiol* 114:653–660
- McCullough DE, Girardin P, Mihajlovic M, Aguilera A, Tollenaar M (1994) Influence of N supply on development and dry matter accumulation of an old and a new maize hybrid. *Can J Plant Sci* 74:471–477
- Mercer TR, Mattick JS (2013) Structure and function of long noncoding RNAs in epigenetic regulation. *Nat Struct Mol Biol* 20:300–307. <https://doi.org/10.1038/nsmb.2480>
- Mi G, Chen F, Wu Q, Lai N, Yuan L, Zhang F (2010) Ideotype root architecture for efficient nitrogen acquisition by maize in intensive cropping systems. *Sci China-Life Sci* 53:1369–1373. <https://doi.org/10.1007/s11427-010-4097-y>
- Moll RH, Kamprath EJ, Jackson WA (1982) Analysis and interpretation of factors which contribute to efficiency to nitrogen utilization. *Agron J* 74:562–564
- Moose S, Below FE (2009) Biotechnology approaches to improving maize nitrogen use efficiency. In: Kriz AL, Larkins BA (eds). *Molecular genetic approaches to maize improvement*. Springer, Berlin. Volume 63. Part II
- Muers M (2011) RNA: Genome-wide views of long non-coding RNAs. *Nat Rev Genet* 12(11):742–743. <https://doi.org/10.1038/nrg3088>
- Naeem MA, Khalid M, Aon M, Abbas G, Amjad M, Murtaza B, Khan WUD, Ahmad N (2018) Combined application of biochar with compost and fertilizer improves soil properties and grain yield of maize. *J Plant Nutr* 41(1):112–122
- Pan X, Abdulaha-Al Baquy M, Guan P, Yan J, Wang R, Xu R, Xie L (2020) Effect of soil acidification on the growth and nitrogen use efficiency of maize in Ultisols. *J Soils Sediments* 20(3):1435–1445
- Parnell JJ, Berka R, Young HA, Sturino JM, Kang Y, Barnhart DM, DiLeo MV (2016) From the lab to the farm: an industrial perspective of plant beneficial microorganisms. *Front Plant Sci* 7:1110
- Pe a PA, Quach T, Sato S, Ge Z, Nersesian N, Changa T, Dweikat I, Soundararajan M, Clemente TE (2017) Expression of the maize Dof1 transcription factor in wheat and sorghum. *Front Plant Sci* 8:434
- Pestsova E, Lichtblau D, Wever C, Presterl T, Bolduan T, Ouzunova M, Westhoff P (2016) QTL mapping of seedling root traits associated with nitrogen and water use efficiency in maize. *Euphytica* 209(3):585–602
- Pingali PL, Pandey S (2001) Meeting world maize needs: technological opportunities and priorities for the public sector. In: Pingali PL (ed) 1999/2000 world maize facts and trends. CIMMYT, Mexico. pp 1–24
- Pii Y, Alessandrini M, Dall'Osto L, Guardini K, Prinsi B, Espen L, Zamboni A, Varanini Z (2016) Time-resolved investigation of molecular components involved in the induction of NO–3NO3– high affinity transport system in maize roots. *Front Plant Sci* 7:1657. <https://doi.org/10.3389/fpls.2016.01657>
- Prinsi B, Espen (2015) Mineral nitrogen sources differently affect root glutamine synthetase isoforms and amino acid balance among organs in maize. *BMC Plant Biol* 15:96
- Qi X, Xie S, Liu Y, Yi F, Yu J (2013) Genome-wide annotation of genes and noncoding RNAs of foxtail millet in response to simulated drought stress by deep sequencing. *Plant Mol Biol* 83:459–473. <https://doi.org/10.1007/s11103-013-0104-6>
- Qi D, Hu T, Song X, Zhang M (2019) Effect of nitrogen supply method on root growth and grain yield of maize under alternate partial root-zone irrigation. *Sci Rep* 9(1):1–10
- Raun WR, Johnson GV (1999) Improving nitrogen use efficiency for cereal production. *Agron J* 91:357–363
- Ribaut JM, Fracheboud Y, Monneveux P, Banzinger M, Vargas M, Jiang C (2007) Quantitative trait loci for yield and correlated traits under high and low soil nitrogen conditions in tropical maize. *Mol Breeding* 20:15–29
- Rostami M, Koocheki AR, Mahallati MN, Kafi M (2008) Evaluation of chlorophyll meter (SPAD) for prediction of nitrogen status in corn (*Zea mays* L.). *American-Eurasian J Agricu Environ Sci* 3(1):79–85
- Saengwilai P, Tian X, Lynch JP (2014) Low crown root number enhances nitrogen acquisition from low-nitrogen soils in maize. *Plant Physiol* 166:581–589. <https://doi.org/10.1104/pp.113.232603>
- Sakakibara H, Takei K, Hirose N (2006) Interactions between nitrogen and cytokinin in the regulation of metabolism and development. *Trends Plant Sci* 11:440–448
- Sandhu N, Sethi M, Kumar A, Dang D, Singh J, Chhuneja P (2021) Biochemical and Genetic Approaches Improving Nitrogen Use Efficiency in Cereal Crops: A Review. *Front Plant Sci* 12:757
- Santi S, Locci G, Monte R, Pinton R, Varanini Z (2003) Induction of nitrate uptake in maize roots: expression of a putative high-affinity nitrate transporter and plasma membrane H⁺-ATPase isoforms. *J. EXP. Bot* 54:1851–1864
- Santos AD, Amaral J nior ATD, Fritsche-Neto R, Kamphorst SH, Ferreira FRA, Amaral JFTD, Vivas JMS, Santos PHAD, Lima VJD, Khan S, Schmitt KFM (2019) Relative importance of gene effects for nitrogen-use efficiency in popcorn. *PLoS ONE* 14(9):e0222726
- Schl ter U, Mascher M, Colmsee C, Scholz U, Br utigam A, Fahnenstich H, Sonnewald U (2012) Maize source leaf adaptation to nitrogen deficiency affects not only nitrogen and carbon metabolism but also control of phosphate homeostasis. *Plant Physiol* 160:1384–1406
- Sekhon RS, Lin H, Childs KL, Hansey CN, Buell CR, Leon ND, Kaeppeler SM (2011) Genome-wide atlas of transcription during maize development. *Plant J* 66:553–563

- Shaner DL, Boyer JS (1976) Nitrate reductase activity in maize (*Zea mays* L.) leaves: II. regulation by nitrate flux at low leaf water potential. *Plant Physiol* 58:505–559
- Sheoran S, Kumar S, Kumar P, Meena RS, Rakshit S (2021). Nitrogen fixation in maize: breeding opportunities. *Theor Appl Genet* pp1–18
- Szklarczyk D, Gable AL, Lyon D, Junge A, Wyder S, Huerta-Cepas J, Simonovic M, Doncheva NT, Morris JH, Bork P, Jensen LJ (2019) STRING v11: protein–protein association networks with increased coverage, supporting functional discovery in genome-wide experimental datasets. *Nucleic Acids Res* 47(D1):607–613. <https://doi.org/10.1093/nar/gky1131>
- Tadesse Ertiro B, Olsen M, Das B, Gowda M, Labuschagne M (2020) Genetic dissection of grain yield and agronomic traits in maize under optimum and low-nitrogen stressed environments. *Int J Mol Sci* 21(2):543
- Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. *Nature* 418:671–677
- Torbert HA, Potter KN, Morrison JE Jr (2011) Tillage system, fertilizer nitrogen rate, and timing effect on corn yields in the Texas Blackland Prairie. *Agron J* 93:1119–1124
- Toubiana D, Fernie AR, Nikoloski Z, Fait A (2013) Network analysis: tackling complex data to study plant metabolism. *Trends Biotechnol* 31:29–36
- Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2013) Maize root growth angles become steeper under low N conditions. *Field Crops Res* 140:18–31. <https://doi.org/10.1016/j.fcr.2012.09.010>
- Trevisan S, Borsa P, Botton A, Varotto S, Malagoli M, Ruperti B, Quaggiotti S (2008) Expression of two maize putative nitrate transporters in response to nitrate and sugar availability. *Plant Biol (stuttg)* 10:462–475
- Tuberosa R, Salvi S, Sanguineti MC, Maccafferri M, Giuliani S, Landi P (2003) Searching for quantitative trait loci controlling root traits in maize: a critical appraisal. *Plant Soil* 255:35–54. <https://doi.org/10.1023/a:1026146>
- U.S. Bureau of the Census. 2009. Current Population Projections. www.census.gov/.
- Uhart SA, Andrade FH (1995) Nitrogen and carbon accumulation and remobilization during grain filling in maize under different source/sink ratios. *Crop Sci* 35:183–190
- Van Oosten MJ, Dell'Aversana E, Ruggiero A, Cirillo V, Gibon Y, Woodrow P, Maggio A, Carillo P (2019) Omeprazole treatment enhances nitrogen use efficiency through increased nitrogen uptake and assimilation in corn. *Front Plant Sci* 10:1507
- Virlet N, Sabermanesh K, Sadeghi-Tehran P, Hawkesford MJ (2017) Field Scanalyzer: an automated robotic field phenotyping platform for detailed crop monitoring. *Funct Plant Biol* 44(1):143–153
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87–115
- Wan TENG, Xue HE, Tong YP (2017) Transgenic approaches for improving use efficiency of nitrogen, phosphorus and potassium in crops. *J Integr Agric* 16(12):2657–2673
- Wang H, Chung PJ, Liu J, Jang I, Kean MJ, Xu J, Chua N (2014) Genome-wide identification of long noncoding natural antisense transcripts and their responses to light in *Arabidopsis*. *Genome Res* 24:444–453. <https://doi.org/10.1101/gr.165555.113>
- Wang RC, Okamoto M, Xing XJ, Crawford NM (2003) Microarray analysis of the nitrate response in *Arabidopsis* roots and shoots reveals over 1000 rapidly responding genes and new linkages to glucose, trehalose-6-phosphate, iron, and sulfate metabolism. *Plant Physiol* 132:556–567
- Wang RC, Guegler K, LaBrie ST, Crawford NM (2000) Genomic analysis of a nutrient response in *Arabidopsis* reveals diverse expression patterns and novel metabolic and potential regulatory genes induced by nitrate. *Plant Cell* 12:1491–1509
- Wang Y, Janz B, Engedal T, de Neergaard A (2017) Effect of irrigation regimes and nitrogen rates on water use efficiency and nitrogen uptake in maize. *Agric Water Manag* 179:271–276
- Wang Z, Ma BL, Yu X, Gao J, Sun J, Su Z, Yu S (2019) Physiological Basis of Heterosis for Nitrogen Use Efficiency of Maize. *Sci Rep* 9(1):1–11
- Wen ZY, Tyerman SD, Dechorgnat J, Ovchinnikova E, Dhugga KS, Kaiser BN (2017) Maize NPF6 proteins are homologs of *Arabidopsis* CHL1 that are selective for both nitrate and chloride. *Plant Cell*. <https://doi.org/10.1105/tpc.16.00724>
- Wen Z, Kaiser BN (2018) Unraveling the functional role of NPF6 transporters. *Front Plant Sci* 9:973
- White PJ, Brown PH (2010) Plant nutrition for sustainable development and global health. *Ann Bot* 105:1073–1080. <https://doi.org/10.1093/aob/mcq085>
- Wu P, Liu F, Li H, Cai T, Zhang P, Jia Z (2021) Suitable fertilizer application depth can increase nitrogen use efficiency and maize yield by reducing gaseous nitrogen losses. *Sci Total Environ* 27:146787
- Yan P, Pan J, Zhang W, Shi J, Chen X, Cui Z (2017) A high plant density reduces the ability of maize to use soil nitrogen. *PLoS ONE* 12(2):e0172717
- Yanagisawa S, Akiyama A, Kisaka H, Uchimiya H, Miwa T (2004) Metabolic engineering with Dof1 transcription factor in plants: Improved nitrogen assimilation and growth under low-nitrogen conditions. *Proc Natl AcadSci USA* 101:7833–7838
- Yang XS, Wu JR, Ziegler TE, Yang X, Zayed A, Rajani MS, Zhou DF, Basra AS, Schachtman DP, Peng MS et al (2010) Gene expression biomarkers provide sensitive indicators of in planta nitrogen status in maize. *Plant Physiol* 157:1841–1852
- Yang JT, Schneider HM, Brown KM, Lynch JP (2019) Genotypic variation and nitrogen stress effects on root anatomy in maize are node-specific. *J Exp Bot* 70(19):5311–5325
- Zamboni A, Astolfi S, Zuchi S, Pii Y, Guardini K, Tononi P, Varanini Z (2014) Nitrate induction triggers different transcriptional changes in a high and a low nitrogen use efficiency maize inbred line. *J Integr Plant Biol* 56:1080–1094
- Zanin L, Tomasi N, Zamboni A, Varanini Z, Pinton R (2015) The urease inhibitor NBPT negatively affects DUR3-mediated uptake and assimilation of urea in maize roots. *Front Plant Sci* 6:1007. <https://doi.org/10.3389/fpls.2015.01007>
- Zhang J, Barber SA (1993) Corn root distribution between ammonium fertilized and unfertilized soil. *Soil Science and Plant Anal.* 24: 411–419. *Frontiers in Plant Science* 12:Agromy11
- Zheng ZP, Liu XH (2013) QTL identification of ear leaf morphometric traits under different nitrogen regimes in maize. *Genet Mol Res* 12(4):4342–4351

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.