Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems

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Abstract

Better management of synthetic nitrogen (N) fertilizers in conventional agricultural systems laid the foundation for feeding the increasing world's population since the Green Revolution. However, excessive reliance on inorganic fertilizer has resulted in environmental degradation issues. Difficulties in soil nutrition management in organic cropping systems often results in lower and variable yields, also raising questions of sustainability. Improving nitrogen use efficiency (NUE) is thus of key importance to overcome environmental concerns in conventional systems and production limitations in organic systems. The differences in the two farming systems have impacts on crop traits and N cycles, making it difficult to enhance NUE with a single strategy. Different approaches need to be adopted to improve NUE in each system. Extensive efforts have been made to better understand mechanisms to potentially improve NUE in cereal crops under both systems. This review suggests that NUE may be improved through a combination of management practices and breeding strategies specific to the management system. Diversified crop rotations with legumes are effective practices to optimize the N cycle in both conventional and organic systems. Best Management Practices coupled with nitrification inhibitors, controlled release products and split-application practices can reduce N loss in conventional systems. In organic systems, we need to take advantage of available N sources and adapt practices such as no-tillage, cover crops, and catch crops. Utilization of beneficial soil microorganisms is fundamental to optimizing availability of soil N. Estimation of soil organic matter mineralization using prediction models may be useful to enhance NUE if models are calibrated for target environments. Cereal crops are often bred under optimum N conditions and may not perform well under low N conditions. Thus, breeders can integrate genetic and phenotypic information to develop cultivars adapted to specific environments and cultivation practices. The proper choice and integration of strategies can synchronize N demand and supply within a system, resulting in reduced risk of N loss while improving NUE in both conventional and organic systems.

Key words: nitrogen use efficiency (NUE), nitrogen cycle, nitrogen loss, organic agriculture, cereals

Introduction of Nitrogen Use Efficiency (NUE) in Conventional and Organic Agriculture

Nitrogen (N) fertilization is integral to the steady increase in global cereal production since the Green Revolution. The global demand for N fertilizer was 115 million metric tons (MMT) in 2015, and the fertilizer use is projected to increase to 236 MMT by 2050 to meet global demands (Pathak et al., 2011; Food and Agriculture Organization of the United Nations [FAO], 2015). Despite increased application of N fertilizer, a large amount is lost and/or unavailable to crop plants in most current agricultural systems. The estimated N recovery in crops during the first year of fertilizer application ranges from 25 to 50%. Applied N losses include loss into ground water, gaseous loss through volatilization and denitrification, immobilization within the soil
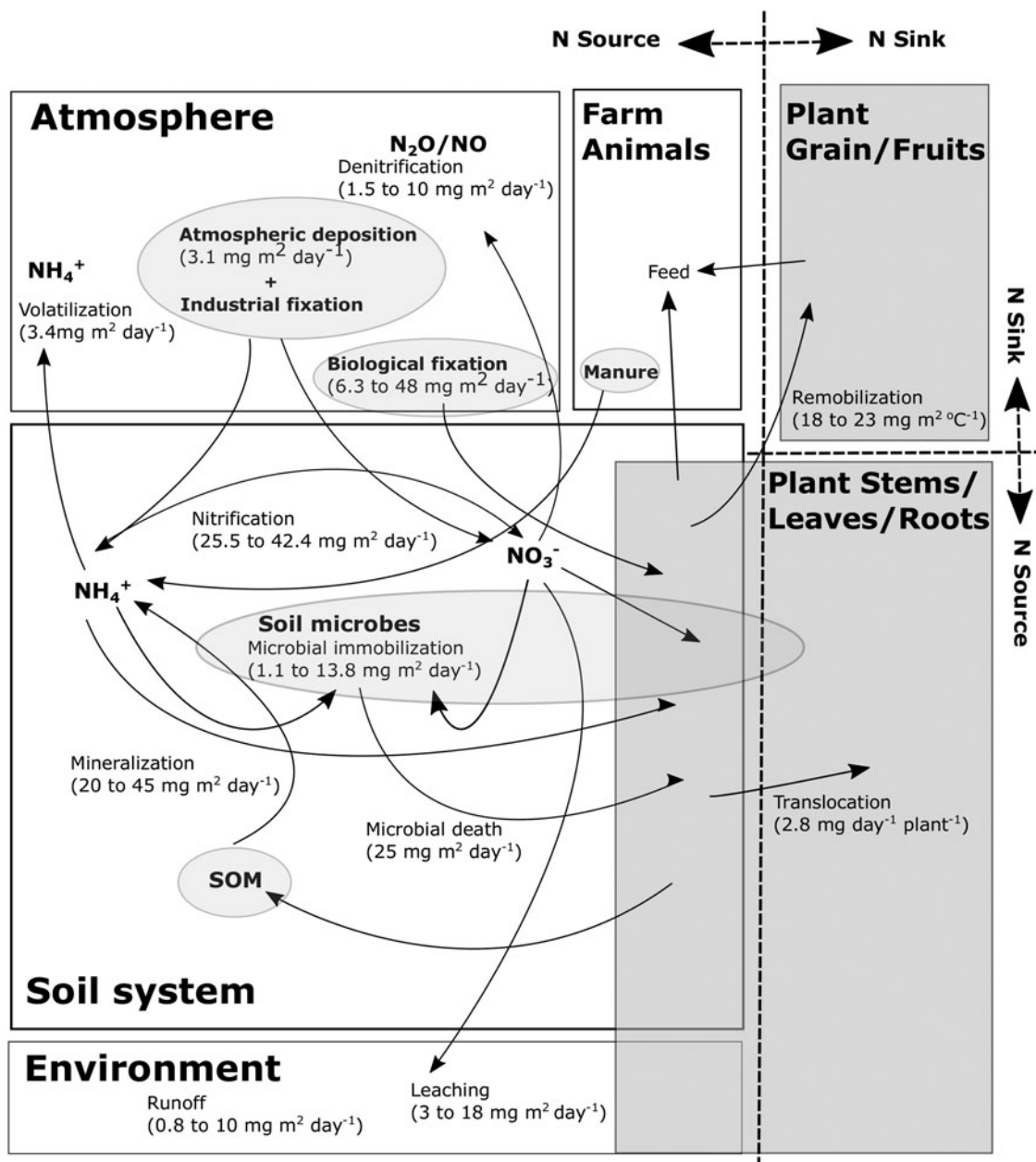
Figure 1. Schematic diagram of nitrogen dynamics in agroecosystems. An example of the amount of nitrogen dynamics in each nitrogen reserve is indicated in parentheses. Boxes with white color indicate environment, whereas dark gray ones refer to plant. Example values are obtained from previous studies (Simpson et al., 1982; Wu et al., 1997; Cabrera et al., 2005; Gooding et al., 2005; Herridge et al., 2008; Dijkstra et al., 2009; Zhao et al., 2011).

system, or limits of plant uptake capacity (Fig. 1) (Robertson, 1997; Raun and Johnson, 1999; Pathak et al., 2011). These N losses into the environment result in serious problems such as water pollution, increased greenhouse gas emissions, altered global N cycles and consequent vegetative alteration (Frink et al., 1999; Horrigan et al., 2002). Also, the production of synthetic N fertilizer requires a significant amount of non-renewable natural gas (Vance, 2001). Transportation and application of the synthetic fertilizer add extra non-renewable energy consumption. Additionally, the use of synthetic

fertilizer on the soil over a longer period of time may affect its ability to sustain healthy plant growth and crop production (Lim et al., 2015). Therefore, our continuing overdependence on synthetic N for cereal production is not sustainable.

Accordingly, there is a growing interest in improving nitrogen use efficiency (NUE) in modern agriculture to reduce associated problems without adversely affecting grain yield. Increased NUE would also benefit primary producers as N fertilization is one of the major costs in crop production, especially in developing countries

(Masclaux-Daubresse et al., 2010). According to an estimate, a 1% improvement in cereal NUE could save more than US$200 million in N fertilizer costs globally (Raun and Johnson, 1999). Organic agriculture has become a major food production system over the last few decades partly because of the perceived environmental and health concerns related to high-input conventional agricultural practices. Organic agriculture is 'a production system that sustains the health of soils, ecosystems and people. It relies on ecological processes, biodiversity and cycles adapted to local conditions, rather than the use of inputs with adverse effects' (International Federation of Organic Agriculture Movement [IFOAM], 2008). Therefore, organic systems primarily rely on nutrition supplied from natural agroecosystems, which are highly variable N supply capability and dynamic. Organic soils often have low N levels, despite high N retention capability on a long-term basis due to higher soil organic matter (SOM) and soil microbial diversity, than soils in conventional systems (Mäder et al., 2002; Pimentel et al., 2005).

One of the overall goals of NUE improvement in grain production is to increase grain yield per unit of N in soil. Variation of grain yield associated with NUE may be altered through genotypic selection (Van Sanford and MacKown, 1986; Huggins and Pan, 1993; Sinebo et al., 2004; Muurinen et al., 2007), agricultural management (Spargo et al., 2008; Khalil et al., 2009a; Sainju et al., 2009), rates, kinds and timing of N applied (Ortiz-Monasterio et al., 1997), climate conditions (Sinebo et al., 2004; Muurinen et al., 2007) and soil properties (Meisinger et al., 1985; Spargo et al., 2008). Some studies suggest that NUE can be improved to obtain higher grain yield in both conventional and organic systems. Several reviews on different aspects of NUE have been published (Raun and Johnson, 1999; Bassirirad, 2006; Dawson et al., 2008; Pathak et al., 2011).

Despite the significant contribution of NUE to crop productivity and the environment, understanding of the detailed mechanisms to improve NUE is relatively limited due to inherent complexity (Basra and Goyal, 2002). Especially, there is limited knowledge on the comparison of various aspects of NUE in conventional and organic production systems. Therefore, the purpose of this review is to present an overall examination of genetic, physiological and agronomical aspects of NUE and related traits under conventional and organic systems. We also propose a possible integrated approach of breeding and agronomic practices to improve NUE in both systems.

Definition and Concept of NUE

The N cycle in agricultural systems is affected by many factors such as soil N concentration, soil chemical, physical and biological properties, crop species and climatic conditions. The manipulation of N movement between N sinks and sources within a plant and an entire ecosystem is a critical component of NUE improvement. Moll et al. (1982) defined the basic concept of NUE as the plant's ability to take up N efficiently from the soil and to partition absorbed N for grain production. Thus, NUE is expressed as the ratio of grain dry matter (Gw) to all N supplied from all available N sources (Ns) (Moll et al., 1982). Applied N fertilizer is often used as Ns because of the difficulties associated with measuring plant available N from mineralization through soil microbial activities. The amount of N loss is also often not accounted for in the calculation. The notion of N source and sink is interchangeable depending on research areas on NUE improvement. For instance, considering soil systems as N sources and crops as N sinks negates the non-linear reality that crops eventually become N sources, etcetera. In addition, a soil system itself could simultaneously become both sink and source; soil microbial immobilization as N sink and inorganic N release from SOM as N source (Havlin et al., 2014). Nitrogen exchange between N sink and source in the individual plant also exists in N metabolic processes according to plant growth (Fig. 1).

Owing to the involvement of complex traits in the concept of NUE, several parameters, which support the explanation of NUE, have been proposed (Table 1). First, NUE has been further divided into two primary components to illustrate the plant's ability to absorb available soil N and to partition N (Moll et al., 1982). Nitrogen uptake efficiency (NupE) reflects a crop's ability to absorb N and is defined as the ratio of total aboveground N (N_t) in the plant at maturity to supplied N (N_s) during the growing season. Nitrogen utilization efficiency (NutE) is an index of the N partitioning ability in the plant, defined as the ratio of grain yield (weight) (G_w) to total N (N_t) in the plant (Moll et al., 1982). For these parameters, the N sink is the entire plant for NupE and grain for NutE, whereas the N source is all plant available N, including applied fertilizer and SOM degradation for both NupE and NutE.

Variation in NupE is caused by genetic, soil, climatic and several agronomic factors (e.g. tillage, irrigation, timing and placement of N fertilizer) and their interaction (Huggins and Pan, 2003; Sinebo et al., 2004). Huggins and Pan (1993) reported the importance of applied soil N levels to NupE. For instance, the contribution of applied N to grain N yield became less as the amount of the applied N increased, even though NupE increased with increased N application. Huggins and Pan (2003) reviewed results of several previous studies and concluded that the decreased contribution of increased N use to NupE was unsynchronized crop N demand and N supply of N fertilizer and N mineralization. In other words, when N is applied over the soil storing capacity, N is lost from the system unless N demand of crop is high and synchronized with crop N demand to utilize an optimum quantity of applied N.

The NutE is another important parameter describing NUE. In a broader sense, NutE explains the plants'

Table 1. Common parameters used for describing nitrogen (N) use efficiency.

NUE parameter	Description
Nitrogen use efficiency (NUE) Dawson et al. (2008)	Grain dry biomass at harvest per plant available N (applied N fertilizer + plant available soil N)
Nitrogen uptake efficiency (NupE) Dawson et al. (2008)	Total aboveground N per plant available N (applied N fertilizer + plant available soil N)
Nitrogen utilization efficiency (NutE) Dawson et al. (2008)	Grain weight per the total aboveground N
Nitrogen Harvest Index (NHI) Dawson et al. (2008)	Grain N per the total aboveground N
Nitrogen Remobilization Efficiency (NrE) Bancal (2009)	The ratio of the total N remobilized to grain from vegetative part [the total vegetative N at (NrE) anthesis—the total vegetative N at maturity] to the total vegetative N at anthesis

ability to produce grain per unit of the total N in a plant. Optimum NutE is ideal for cereal crops grown in low fertility where plant-available N is limited. Several studies report that the contribution of NutE to overall NUE is not well understood and may not be as significant as NupE in wheat, barley, oats and maize (Presterl et al., 2002; Sinebo et al., 2004; Muurinen et al., 2006; Sylvester-Bradley and Kindred, 2009). In general, a crop species or cultivar has a unique N optimum utilization threshold, and crop internal N and grain yield do not increase in direct proportion to applied N (Sylvester-Bradley and Kindred, 2009). In addition, quality traits such as grain protein are very important for wheat and barley producers. Increased NutE may lead to lower grain protein concentration due to N dilution effects when nitrogen harvest index (NHI: N in grain/N in total biomass) remains the same (Huggins and Pan, 2003). Isfan (1993) suggested that increased NutE may be an important trait to consider when developing high NUE cultivars for limited N conditions typically found on organic farms. Greater NutE might be achieved through either improvement of N remobilization efficiency (NrE) or maintaining active photosynthesis (Masclaux-Daubresse et al., 2010). Fertilization rates and regimes also affect wheat NrE, which is affected by specific enzymatic activity (Habash et al., 2001; Miflin and Habash, 2002; Forde and Lea, 2007; Bancal, 2009). Therefore, the effects of fertilizer managements on NutE cannot be ignored. Similar to NutE, NHI represents the translocation efficiency of acquired N for grain protein accumulation (Dawson et al., 2008). This parameter is of particular importance in choosing parental cultivars for wheat breeding because the protein content in wheat grain directly affects grain price, and is of great importance to producers. High NHI levels indicate an efficient N utilization/translocation; thus cultivars with high NHI requires less N to produce similar yield as those with low NHI (Spiertz and De Vos, 1983).

Improvement of NUE for Mitigating Environmental Issues

The highly productive cereal production systems have negatively impacted environment through exploitation of non-renewable resources, ground fresh water pollution and eutrophication (Glibert et al., 2006). The relationship between yield and consumption of N fertilizer is non-linear (Sowers et al., 1994). Thus, the challenge in most of the agricultural systems is to find the means to improve efficiency of N fertilizer for sustainable food production. Mitigating the inefficiency of N fertilization has also a potential to slow down climate change through reducing emission of major greenhouse gases. Among these, nitrous oxide (N_2O) emission from soil is mainly related to the excess amount of N fertilizer (Fig. 1); therefore, improved NUE in agriculture would reduce N_2O emission. Liu et al. (2016) wrote a comprehensive review on the sustainable farming practices that could impede climate change through reducing carbon (C) footprints. In a study, direct and indirect N_2O emission from cereal production was found to be 12 times higher in 2011 compared with 1970, while NUE decreased by approximately 74% in that period in Brazil (Amanullah et al., 2016). The authors attributed these results to increased consumption of N fertilizer and predicted that an increase in NUE by 2.4% from current figure would reduce use of N fertilizer worth US$21 million, resulting in reduced N_2O emission (Amanullah et al., 2016). A meta-analysis of 19 published studies indicated that N_2O emission per unit of harvested product, called yield-scaled N_2O emission, reduced 12.7–7.1 g N_2O-N kg^{-1} N uptake with an increase of NUE from 19 to 75% (Sowers et al., 1994). It is challenging to breed genotypes with 50% greater NUE than current genotypes in a short time; however, it may be realistic to improve crop NUE up to 50% with minimizing yield loss as NUE is largely controlled by phenotypic variations (Table 2).

Inorganic fertilizer or manure application is prone to leaching or runoff, resulting in the environmental issues, when not properly applied under water and tillage managements. In a semi-arid irrigation practice, increasing N fertilization over 150 kg ha^{-1} did not increase maize yield due to reduction in NUE, and increased the risk of N leaching under irrigation (Gholamhoseini et al., 2013). All kinds of N inputs are vulnerable to loss in the environment when not incorporated into the soil (Eghball and Gilley, 1999).

Table 2. Examples of nitrogen use efficiency (NUE)[1], uptake (NupE) and utilization efficiency (NutE) in cereals.

Crops	NUE kg kg^{-1} High N	NUE kg kg^{-1} Low N	NupE kg kg^{-1} High N	NupE kg kg^{-1} Low N	NutE kg kg^{-1} High N	NutE kg kg^{-1} Low N	N fertilization	Tested materials	References
Wheat	18–38	41–101	0.74–0.92	1.14–1.35	27–39	41–59	Two levels	Registered and advanced breeding line winter variety	Gaju et al. (2011)
	Conventional: 27	Organic: 19	NA		NA		fertilized in conventional and legume-based rotation in organic	Registered winter variety	Swain et al. (2014)
	26–44		NA		31–42		Four N levels	CIMMYT historical variety	Ortize-Monasterio et al. (1997)
Maize	5–32	21–110	0.17–0.99	0.75–2.59	11–54	16–59	Two levels	Recombinant inbred lines and Parents	Li et al. (2015)
	33–52		NA		NA		Five N levels including foliar fertilization and control	Hybrid	Kalinova et al. (2014)
	25–44		0.36–0.58		110–167[2]		Two N levels and control with different row spacing	Hybrid	Barbieri et al. (2008)
Rice	9–15		0.27–0.53		8–19		Four different split-plot combinations with the same total N and control	Hybrid	Sun et al. (2012)
	12–18		0.34–0.53		8–20		Three different panicle N application with the same basal N application and control		
	Dry season crop: 29	Wet season crop: 64	NA		NA		No fertilization	IRRI variety	Cassman et al. (1996)
Barley	13–31		0.38–0.92		26–43		One level with split-application and control	Breeding lines	Sinebo et al. (2004)
	35–58		NA		NA		Fertilized	Multiple crosses + registered variety	Anbessa et al. (2009)

[1] These NUE values are obtained from only studies in which NUE was calculated as Gw/Na (N applied + /or initial soil N).
[2] The values are obtained as the ratio between the total aboveground DM and N in the DM.

NUE in Conventional and Organic Agriculture

Physiology and genetics of NUE

To overcome the complex and quantitative manner of endogenous and exogenous mechanisms in NUE-related traits, understanding the genetic basis of N metabolism is essential for improving NUE. All components involved in NUE-related gene expression and metabolic pathways, controlling N uptake, utilization, partitioning and recycling are the subject of physiology, genetic and molecular studies. Most grain crops store a large pool of absorbed N during the vegetative stage and recycle pooled N during the reproductive stage when post-anthesis N uptake declines. In wheat, 50–90% of N in grain is derived from pooled N in stems and leaves (Spiertz and De Vos, 1983; Kichey et al., 2007). Therefore, systems in the pathways of N assimilation, remobilization and re-assimilation must be regulated according to external and internal N status to improve NUE. These metabolic pathways are controlled by complex genomic and consequent physiological steps in association with environmental factors that result in phenotypic characteristics. While N availability is mostly determined by environmental conditions and agronomic practices, the quantity of N intake into the root cytoplasm is regulated by passive and active uptake mechanisms controlled by several plant genes (Schenk, 1996; Tinker and Nye, 2000). Passive absorption usually refers to mass flow and diffusion, occurring along transpiration and energy gradients, respectively (Havlin et al., 2014). Active uptake occurs against concentration gradients through energy-required enzymatically driven actions. Thus, attempts to improve NupE through modifying root kinetics have been proposed (Bassirirad, 2006). The nature of uptake kinetics is mediated by genetically regulated active membrane transporters. Nitrate transporters (NRT) from the NRF and NRT2 families, and ammonium transporters have been identified for absorption and translocation of nitrate and ammonium (Dechorgnat et al., 2011; Nacry et al., 2013; Léran et al., 2014). Plants selectively use these transporter systems to absorb nitrate and ammonium, depending on their concentration in soil solutions. A high-affinity transporter system (HATS) works when nitrate and ammonium concentrations are lower than 1 mM, while a low-affinity transporter system (LATS) becomes predominant when concentrations are higher than 1 mM (Dechorgnat et al., 2011; Nacry et al., 2013). Extensive studies have been conducted to characterize genes involved in these transporter systems as well as the functions of those genes (Vidmar et al., 2000; Orsel et al., 2002; Plett et al., 2010; Léran et al., 2014). Exploring functional mechanism of gene families NRF and NRT2, which are responsible for the activities of LATS and HATS, respectively, is the first step toward improving N uptake and specifically nitrate uptake in plants. The HATS system is further divided into constitutive HATS (cHATS) and inducible HATS (iHATS) (Behl et al., 1988; Aslam et al., 1992). Attempts to increase N uptake through overexpressing these gene families resulted in improved nitrate influx under some conditions, but failed to improve NUE in *Arabidopsis thaliana* and tobacco plants (Fraisier et al., 2000; Pathak et al., 2008). This may suggest that improvement of NUE is not always source limited and improved N uptake can be successful to improve NUE when polygenetic functions involved in N metabolism pathways are taken into account for NUE enforcement.

During the vegetative stage, a large pool of absorbed nitrate is assimilated into roots and shoots. During this process of assimilation, nitrate is firstly reduced to nitrite in the cytoplasm by an enzyme called nitrate reductase (NR), and then further reduced to ammonium by nitrite reductase (NiR) in the chloroplast (Dechorgnat et al., 2011). The ammonium produced by NiR and ammonium from soil solutions and photorespiration is finally transported through phloem sap in the phloem and stored in each part of the plant's body as different forms of amino acids. The amount and the place for storing these amino acids depend on the plant species and the amount of available nitrate in soil solutions (Christophe et al., 2011). Assimilated N is stored as some form of amino acid or protein in plant organelles, which later becomes a source for N remobilization. Because NR is the first enzyme involved in N assimilation where nitrate is the N source, it was thought that the variability of NR activity is rate limiting and a key to increasing NUE in maize and growth of tobacco (Sherrard et al., 1986; Quilleré et al., 1994; Hirel et al., 2001; Masclaux et al., 2001). In maize, a high variability of NR activity was observed and was used to increase grain yield through traditional breeding techniques (Sherrard et al., 1986). In transformed *Nicotiana plumbaginifolia*, which overexpresses NR, NR activity in leaves increased 25–150% than that of the wild-type, while there was no difference in total N protein and dry matter production between the two types (Quilleré et al., 1994). Since NR is just responsible for the first step of N, increased expression of NR genes in plants with little uptake or storage pool of nitrate may not be an ideal strategy. The enzymes involved in the further assimilation process need to be considered to improve nitrate assimilation.

The second candidate enzyme in the process of nitrate assimilation is glutamine synthetase (GS) (Andrews et al., 2004). Ammonium derived from nitrite reduction and photorespiration is finally synthesized into glutamine by GS. Together with 2-oxoglutarate, glutamine is further catalyzed by the glutamine 2-oxoglutarate aminotransferase (GOGAT) to form glutamate in the plastid and cytoplasm (Masclaux-Daubresse et al., 2010). In major cereal crops, assimilation and remobilisation of N have been widely studied in relation to GS activity (Miflin and Habash, 2002; Masclaux-Daubresse et al., 2010; Bao

et al., 2015). Since the failure of improving crop yield through single enzyme overexpression of NR/NiR (Quilleré et al., 1994; Hirel et al., 2001; Masclaux et al., 2001), GS has been studied to understand the entire enzymatic involvement for improving NUE in cereal crops. Together with glutamate synthetase, GS forms a GS–GOGAT cycle that is responsible for the central role of ammonium assimilation and remobilization from vegetative parts to developing grain in cereal crops (Miflin and Lea, 1977; Miflin and Habash, 2002). Multiple isoforms of GS exist in plants. The number of genes encoding cytosolic GS isoforms varies in wheat (*TaGS1a, TaGS1b* and *TaGS1c* for GS1;1, *TAgsR1* and *TaGSr2* for GS1;2 or GSr, *TaGSe1*, and *TaGSe2* for GS1;3 or GSe) (Bernard et al., 2008), rice (*OsGS1;1, OsGS1;2* and *OsGS1;3*) (Tabuchi et al., 2005) and maize (*Gln1-1, Gln1-2, Gln1-3, Gln1-4* and *Gln1-5*) (Martin et al., 2006), while a gene encoding chloroplast GS has been found in wheat (*TaGS2a, TaGS2b* and *TaGS2c* for GS2) (Bernard et al., 2008; Wang et al., 2015), maize (*Gln2*) (Martin et al., 2006) and rice (*OsGS2*) (Tabuchi et al., 2005). Improvement of reverse genetic techniques and availability of mutant plants have led to our increased knowledge of the specific gene functions related to the GS isoform family (Martin et al., 2006). In maize, double- and single-mutants of *Gln1-3* and *Gln1-4* reduced the expression of GS mRNA in leaves, kernel number per ear and kernel weight, respectively, while not exhibiting a significant reduction of vegetative biomass (Martin et al., 2006). This implies that these two GS isoforms are specifically responsible for grain development but not vegetative growth (Martin et al., 2006). The knockout mutant of *OsGS1;1* showed a severe decline in the total growth of a rice stand and grain filling (Tabuchi et al., 2005). Although the presence of other GS1 genes *OsGS1;2* and *OsGS1;3* in the mutant did not compliment this phenotypic result, re-introduction of *OsGS1;1* cDNA in the mutant led to complementation of these phenotypes (Tabuchi et al., 2005). Therefore *OsGS1;1* could be a pivotal gene for the assimilation of ammonium and the translocation of glutamine to developing rice grains.

Nitrogen remobilization occurs in the process of senescence. During this process, photosynthetic cellular components (e.g. chloroplast) and enzymes (e.g. Rubisco) are mainly dismantled into amino acids, amides and ammonium (Hörtensteiner and Feller, 2002; Gooding et al., 2005). Degraded ammonium is reduced by GS into glutamine. Glutamine is the major amino acid exported through both phloem and xylem to developing grain in barley and wheat. Therefore, the GS gene family plays a critical role in remobilizing necessary N to grain development during leaf senescence in cereal crops (Habash et al., 2001; Miflin and Habash, 2002; Forde and Lea, 2007). At this growth stage, leaves become an N source for protein synthesis in grain while N uptake from roots gradually reduces (Masclaux-

Daubresse et al., 2010). Therefore, efficient N recycling in leaves influences N yield in final harvest products. A positive correlation between GS activity in leaves and grain protein content has been reported in both rice and wheat (Yang et al., 2005; Habash et al., 2007). Therefore, cytosolic GS1 and chloroplast GS2 activities in the flag leaf are considered useful characteristics to evaluate when selecting potential parents for breeding (Obara et al., 2001; Kichey et al., 2007; Fontaine et al., 2009). These three studies suggest that enzymes involved in N assimilation pathways (i.e. NR, NiR, GS and GOGAT) are all coordinated, and a single approach will not efficiently enhance NUE and final yield. However, GS activity appears to play a pivotal role during leaf senescence contributing to increasing NUE (Jain et al., 2011).

Aspects of Management Systems

Strategies to reduce N losses in conventional agriculture

Nitrogen fertilization is the primary source of N leaching and atmospheric nitrogen oxides (NOx) emissions and is estimated to exceed 50% of the global NOx budget by 2025 (Yienger and Levy, 1995). Understanding the proper application of N fertilizer is, therefore, critical to reducing its environmental loading and to improve NUE in the system (Yienger and Levy, 1995). To achieve optimum results, a fertilization strategy, also called the 4Rs of N nutrient management or Best Management Practices (BMPs) for N fertilization, has been proposed (Griffith and Murphy, 1991; Matson et al., 1998; Alva et al., 2011; Ruidisch et al., 2013). The BMPs is a combination of four different concepts of fertilization practices. The practices emphasize a fertilization regime with the right rate and the right timing from the right sources at the right place (Griffith and Murphy, 1991; Alva et al., 2011). Nitrogen dynamics vary with production systems such as organic and conventional, or dry and humid environments. Thus, operation of BMPs requires substantial understanding of on-site N mineralization, immobilization, cycling and N requirement of growing crops (Dawson et al., 2008). Recent studies demonstrate that precision agricultural technologies based on BMPs offer a promising approach to improve NUE (Khosla et al., 2002; Zebarth et al., 2009; Ahrens et al., 2010). A study at a site-specific N management indicated that the key for successful on-farm precision N management is the right choice and timing of N application while taking into account on-farm residual N (Ahrens et al., 2010).

Selection and rate of N fertilizers, placement depth (Khalil et al., 2009a) and timing of application (Malhi et al., 2010) all influence N losses from soil. Different forms of inorganic N fertilizer cause different rate of N loss (Table 3). Urea is one of the most widely applied N

Table 3. Estimation of nitrogen loss by volatilization for various N source and application methods [Cai et al. (2002) and Havlin et al. (2014)].

Fertilizer	Application method	% Ammonia loss by volatilization
Urea/urea-ammonium nitrate	Surface broad cast	0–44
	Deep point placement	0–12
Ammonium sulfate	Surface broad cast	0–60
	Deep point placement	0–30
Ammonium nitrate	Surface broad cast	0–30
	Deep point placement	0–20
Anhydrous ammonia	Injected	0–5

fertilizers accounting for 55% of global N fertilizer consumption due to minimum risk of explosion under storage conditions, easy handling and low cost (Glibert et al., 2006; International Fertilizer Industry Association [IFA], 2011). The share of urea consumption to total N consumption is higher in developing countries than in developed countries (IFA, 2011). Urea is also responsible for a greater amount of ammonia and N_2O emissions than other N fertilizer because of its rapid and easily hydrolyzed nature after application (Khalil et al., 2002; San Francisco et al., 2011). This characteristic causes a significant amount of ammonia to be volatilized and a percentage of nitrate from the ammonia to be denitrified. Application of urea over large physical areas also results in severe N loss.

Nitrogen sources affect crop morphological root development differently. For instance, nitrate promotes elongation of lateral roots, whereas ammonium promotes initiation of lateral roots (Zhou et al., 2009; Lima et al., 2010). Due to this differential response, plants can extend specific roots and efficiently explore different N sources, which selectively promote root development in a large volume of soil. Wang and Below (1992) studied the effect of mixture of nitrate and ammonium fertilizers on morphology of two wheat cultivars. Although no causal relationship of treatment-induced differences was found, they observed a substantial increase in vegetative dry weight and the number of tillers of cultivars with the mixture of these fertilizers (i.e. 75/25, 50/50 and 25/75, NO_3/NH_4), compared with that of cultivars receiving only one form. The two wheat cultivars also responded differently to the different forms of N fertilizer for tiller development; one cultivar produced more tillers with nitrate, whereas the other produced more tillers with ammonium (Wang and Below, 1992). Similarly, yield, development of leaf area, chlorophyll and plant height

differed with N sources in maize (Abbasi et al., 2013; Amanullah et al., 2016). Yield and the growth response of these traits were greater with application of either calcium ammonium nitrate or ammonium sulfate than with urea. These studies indicate that crops and N sources interact to cause various growth responses, thus further studies are needed to take full advantage of choice of N fertilizers for achieving better NUE.

Critical periods of N demand vary in crops and adjusting fertilization timing according to crop N requirements may reduce the risk of N loss and excessive N fertilizer application (Fageria and Baligar, 2005). For instance, the critical timing of N demand in spring wheat is between double ridge to terminal spikelet phases (between 20 and 45 days after seeding) (Limon-Ortega and Villaseñor-Mir, 2006), while in maize it ranges from 35 to 45 days after seeding (Richie et al., 1986). In malting barley, adjusting the amount of split-N application is necessary to ensure good malting quality (Baethgen et al., 1995). López-Bellido et al. (2005) reported that recovery of split-^{15}N fertilizer application in wheat was, on average, 55% in three different N rates when fertilizer was applied as topdressing at terminal spikelet and stem-elongation stages; compared with 14% recovery for one-time application at pre-sowing. Under a winter wheat cultivation system, the plant recovery of ^{15}N-labeled N at booting was greater when applied with split-N fertilization than with one-time fall application (57.4 and 46%, respectively) (Sowers et al., 1994). In many cereal production areas, N application practices are based on soil N analysis at seeding. Although one-time application of all required N at seeding is a common and relatively effective practice for winter wheat production in drier areas (McKenzie et al., 2010), several studies indicated that split-application of N fertilizer (e.g. at seeding, tillering and stem elongation) improved NUE, the total N yield and grain yield in various growing conditions (Spiertz and De Vos, 1983; Limaux et al., 1999; López-Bellido et al., 2005). These results clearly show that the extent of plant N uptake is associated with N demands at different plant growth stages where N is used for cell division and growth, and thus the timing of fertilizer application needs to be synchronized with the timing of crop N requirement.

Besides split-fertilization, application of polymer coated N fertilizers is another useful strategy to synchronize N supply and demand, and reduce N losses (Yanai et al., 1997; Khalil et al., 2009b; Malhi et al., 2010). These fertilizers are covered with different types of polymer coats such as controlled-release compounds or urease and nitrification inhibitors (Havlin et al., 2014). Several studies reported the positive effects of polymer-coated controlled-release N (CRN) on grain yield, NUE (McKenzie et al., 2007; Malhi et al., 2010) and N leaching (Yanai et al., 1997). The release timing of CRN is designed to synchronize N requirement in the plant (Malhi et al., 2010), thereby minimizing the risk of N leaching under normal conditions. For instance, urea is nitrified within 2 weeks under

favorable conditions, whereas anhydrous ammonia is converted to nitrate slower than urea (Nielsen, 2006). The critical timing for N requirement in winter wheat is at the double ridge stage and from tillering to stem elongation, which occurs at the beginning of the spring. Therefore, regular fertilization at the time of seeding does not provide the appropriate amount of N at the proper time in winter wheat. Moreover, a considerable amount of N is lost to the environment during the winter. Therefore, the application of CRN at seeding is especially effective in winter wheat to prevent N loss under wet winter conditions, which tend to result in increased denitrification and N leaching (Malhi et al., 2010). Nevertheless, negative or negligible influence of CRN on NUE has also been reported in the literature (McKenzie et al., 2010). Such inconsistent responses may be caused by year-to-year variation in weather (Malhi et al., 2010; McKenzie et al., 2010).

Split-banded application of urea in spring wheat and barley (half each at seeding and tillering) and canola (at bolting stages) was as effective as the spring-banded application of CRN as a single dose (Malhi et al., 2010). Use of CRN to pots with and without crop reduced the concentration of nitrate in soil solutions at all sampling times, indicating that CRN reduces N leaching (Yanai et al., 1997). These results suggest that CRN and split applications of fertilizer may have theoretically similar effects of reducing N loss and, therefore, improving NUE.

To mitigate soil enzymatic factors affected by environmental variation, the combination of urease and nitrification inhibitors has been tested (Gioacchini et al., 2002; Boeckx et al., 2005). These types of inhibitors are responsible for limiting the enzymatic activities of urea hydrolysis and ammonium nitrification. The use of urease inhibitors leads to increased urea content in the soil, and the use of a nitrification inhibitor increases soil ammonium content (San Francisco et al., 2011). In general, nitrate is more readily lost in the environment than ammonium. Usage of several urease and nitrification inhibitors resulted in some suppression of N losses (Weber et al., 2004). In general, these inhibitors are more effective in reducing N loss when the fertilizers along with inhibitors are applied, under conditions that are prone to volatilization, denitrification and N leaching (Barth et al., 2001). Therefore, results depend on soil and environmental variation (Gioacchini et al., 2002; Boeckx et al., 2005; Khalil et al., 2009b; San Francisco et al., 2011).

In addition to fertilization regimes, the diversification of crops/cropping practices in crop rotation plays a significant role in improving NUE in conventional systems. Diversified crop rotations with leguminous crops take biologically fixed N into the N cycle *in situ*, resulting in the reduction of N fertilizer use. When legume crops were included as preceding crops in a no-till crop rotation, N fertilizer accounted for 42–55% of the total N input in wheat and canola compared with 52–60% of total N

input derived from N fertilizer when preceding crops were non-legumes (Luce et al., 2016). Nitrogen derived from the decomposition of preceding leguminous crops compensated for a portion of the N fertilizer input. When a large volume of N is required for cereal crops, selection of N-fixing crops as preceding crops could reduce N fertilizer application amount, minimizing the risk of N loss in the environment. When succeeding crops were fertilized with the recommended amount of N, increased yield of the following crops are greater than those following non-leguminous crops (Badaruddin and Meyer, 1994; Yadav et al., 2003; O'Donovan et al., 2014; Luce et al., 2015). The amount and timing of available N in legumes depends on factors such as the C/N ratio, tillage practices, soil microbial diversity and climate. Greater care is needed when legumes are incorporated in rotations for reducing N fertilizer.

The inclusion of post-harvest cover crops in crop rotations has been successfully practised throughout the world. Cover crops maintain favorable soil conditions for improving NUE such as adding and conserving N, optimizing the C/N ratio of residues and preventing soil erosion (Dabney et al., 2010). In summer crop farming regions, the use of two winter cover crops affected yield and N uptake of the following maize crop (Gabriel et al., 2016). Barley as a winter cover crop grew faster than vetch; however, vetch finally covered more ground than barley in winter, resulting in high N content in yield biomass (Gabriel et al., 2016). Thus, barley may be used as a means of N conservation in this system as it minimizes the risk of post-harvest N loss and soil erosion. On the other hand, vetch has a greater N contribution to the following crop than barley. A meta-analysis of N dynamics between the diversified rotations and the conventional simple rotations with bare fallow demonstrated that legume-based crop rotations reduced nitrate leaching up to 40% relative to conventional fertilizer-based rotations, indicating that the replacement of bare fallow with legume cover crops provide dual benefits of conserving and adding N (Tonitto et al., 2006). The authors also reported that inclusion of cover crops prevented post-harvest N volatilization and denitrification. In the Northern Plain semiarid area, summer fallow used to be a common practice to store sufficient soil moisture for succeeding crop germination despite the risk of soil erosion and denitrification (Aulakh et al., 1982). Studies of crop diversification in rotations in semiarid regions reported that diversification with pulse/green manure in rotation had the additional benefit of increased water availability for succeeding crops (Gan et al., 2015, 2016). Such a finding provides farmers an alternative practice to conserve soil moisture, replacing summer fallow. Although, long-term studies investigating the direct effect of diversified crop rotations on NUE are few, these studies suggest the importance of crop sequences and diversification of crops in rotations for potential improvement of NUE.

Strategies to Reduce N Loss in Organic Agriculture

Organic agriculture is based on using the existing ecological system and recycling processes. In the absence of synthetic N fertilizer, the primary approach for improving NUE in organic agriculture is to maintain existing residual N, potential N mineralization reserves in the soil and to recycle on-farm materials through green manure, and incorporating plant residues from previous crops (Spiertz and De Vos, 1983; Drinkwater, 2004; IFOAM, 2008). Diverse knowledge, techniques and strategies are required to optimize the utilization of various N reservoirs. Sources of N are mainly derived from on-farm materials, and can be limited, especially in extensive organic farming systems. Therefore, proper management of these reserves in soils is a key management strategy to provide the necessary amount of N to crops. This can be achieved through a combination of crop rotation, incorporation of legume crops as a source of biologically fixed N in the rotation, tillage practices and use of catch crops (Lupwayi et al., 2006; Constantin et al., 2010; Snyder and Spaner, 2010; Doltra and Olesen, 2013). Although these practices are also observed in conventional systems, the contribution of these practices toward NUE is greater in organic systems than in conventional systems (Huggins and Pan, 1993; Drinkwater, 2004).

Organic practices tend to cause less N loss than conventional systems; a combined result attributed to inherent low concentrations of plant available inorganic N, the incorporation of legumes and catch crops and diverse crop rotations (Stopes et al., 2002; Syswerda et al., 2012). For example, annual nitrate loss under organic management was 19 kg N ha^{-1} yr^{-1} compared with 62 kg N ha^{-1} yr^{-1} in conventional systems in one study (Syswerda et al., 2012), and 36 kg N ha^{-1} yr^{-1} in organic systems versus 57 kg N ha^{-1} yr^{-1} in conventional systems in another (Stopes et al., 2002). It may, therefore, be more difficult to increase NUE in organic systems than in conventional.

This suggests that it is even more important to understand the mechanisms contributing to increased NUE in organic systems.

Crop rotation is one of the most important management practices for organic farmers to maintain soil fertility (López-Bellido and López-Bellido, 2001; Eriksen et al., 2004). In western Canada, the typical organic rotation includes legumes and pulses in a several-year rotation that appears to maintain soil N levels due to N fixation of these crops (Degenhardt et al., 2005; Snyder and Spaner, 2010). The choice of crops in rotation depends on weather, soil condition, plant adaptation and market demands but the inclusion of legumes is obviously beneficial to maintain soil N levels. The relationship between crop rotation and NUE/N loss has been extensively studied (Porter et al., 1996; López-Bellido and López-Bellido, 2001; Sainju et al., 2009; Askegaard et al., 2011).

Legumes and their associated N-fixing bacteria are critical components of N supply in organic crop rotation systems. Inclusion of leguminous crops provides atmospheric N to the host plants which eventually store N as SOM for long term. Several studies have reported improvement of soil N status, including potentially mineralizable N, total N and plant available N in legume-based rotation practices (Marriott and Wander, 2006; Kayser et al., 2010). Ammonia fixed through biological means such as legume and N-fixing bacteria provides an important portion of plant required N, partially obviating the need for industrial fertilizers. For instance, endophytic N-fixing bacteria can provide 10–25% of required N in maize and rice (Okon and Labandera-Gonzalez, 1994; Mano and Morisaki, 2008; Figueiredo et al., 2010; Amiri and Rafiee, 2013). Moreover, biologically fixed N is less susceptible to loss than synthetic N fertilizer on a short-term basis due to direct translocation of ammonia from bacteria to their host plants (Ondersteijn et al., 2002). The fixed N is immediately converted into organic forms as amino acids, which assimilate into plant cells and become stable. A study reported that unfertilized wheat following a grain legume crop yields almost the same as wheat with 75 kg N ha^{-1} fertilization although grain N concentration varies according to weather conditions (Badaruddin and Meyer, 1994). Wheat NUE, NupE and NutE were greater after cowpea compared with rice (Yadav et al., 2003). This was caused by the better root growth and crop establishment of wheat coupled with the increase of the soil organic C and available N in the cowpea–wheat rotation. These results demonstrated that including legumes in rotation ensures N availability to succeeding crops. Although availability in legume residual N in rotation is unpredictable and difficult to manage; plough-in legumes or other plant residues are eventually decomposed by soil microorganisms, and released N from these residues is prone to loss when N supply and crop demand are asynchronous (Crews and Peoples, 2005). A key for the rate of N mineralization in plowed legumes is the C/N ratio, weather and soil microbial conditions. Thus timing of plowing, which provides favorable conditions to decomposers, must be considered (Herridge et al., 2008; Kayser et al., 2010). Much of the N pool of grain legumes is removed during harvesting, whereas green manure or cover crop legumes are not grown for grain and inclusion of these non-grain legumes is a better choice for keeping all fixed N within the system. Planting legumes with overlapping life cycle of main crops, also called relay intercropping, is found to be an agronomically and ecologically feasible practice for improving NUE (Jeranyama et al., 1998). Although competition between legumes and winter wheat for resources caused reduction of grain protein in wheat grain after relay intercropping, the yield of subsequent crops increased due to leguminous soil N enrichment (Amossé et al., 2013, 2014).

Tillage remains necessary in organic systems especially for weed control. Tillage provides necessary aeration and

optimum moisture and is, therefore, very important to the microbial decomposition of SOM. However, tillage may cause severe N losses through N leaching or soil erosion (Kessavalou et al., 1998; Sainju et al., 2009). Due, in part, to N conservation awareness and increased fuel costs, no-till has been widely implemented in conventional systems to conserve N pools (Porter et al., 1996; Spargo et al., 2008). Organic matter derived from plant residues accumulates on the surface. Plant available N is immobilized into organic forms by diverse soil microorganisms around the surface soil under no-till managements (Doran et al., 1998), whereas an increase in N loss through leaching, volatilization and denitrification was observed as the frequency and intensity of tillage increased (Sainju et al., 2009). Another study noted that no-till maintained a larger amount of soil nitrate concentration than the conventional tillage system (Lupwayi et al., 2006). This may be because long-term conservation (reduced or no) tillage systems preserve habitat for soil microbial communities and promote accumulation of soil enzymes responsible for N dynamics. Since most soil enzymes are of microbial origin (Gianfreda et al., 2011), maintaining soil microbial communities in no-till systems has a great impact on soil enzyme activities, thus affecting N mineralization (Muruganandam et al., 2009). Nitrate and ammonium produced through microbial mineralization may simultaneously immobilize due to the rapid turnover of microbial biomass under the high C/N ratio in soil (Muruganandam et al., 2010). Immobilization of N caused by no-till is in balance with N mineralization; thus no-tillage practice may be more efficient from a sustainable standpoint (House et al., 1984; Muruganandam et al., 2010). Franzluebbers (2004) estimated the amount of soil organic N in several tillage treatments in the previous studies and found that the total organic N in no-till managements is 23 kg N ha^{-1} yr^{-1} higher compared with plow tillage. However, the effect of no-till on limiting N losses is mostly controlled by soil and weather conditions (Hansen and Djurhuus, 1997), and may be less effective in limiting N loss than catch crops or timing of tillage (Constantin et al., 2010). Finding mechanisms to incorporate no or limited tillage systems into organic management strategies is needed.

Depending on soil fertilization regimes, the rate of N uptake during the crop growing season is generally higher than the rate of N mineralization in organic fields and the risk of N loss is low in most cases (Watkins and Barraclough, 1996; Masunga et al., 2016). However, a high risk of N leaching could become a problem in bare fields after harvest, especially when the temperature in a fallow season is relatively high and the field is left uncropped (Stopes et al., 2002; Eriksen et al., 2004). This leaching is due to a combination of increased activity of decomposers and the absence of crop to trap N. The use of a catch crop after the main crop harvest has a potential role in reducing the risk of N leaching

during the off-season (i.e. fall and winter). Catch crops absorb N in the soil and store N, thus preventing N leaching. The stored N as SOM is eventually decomposed in the next crop season. A long-term study was conducted to evaluate the effect of cover crop on the reduction of soil N loss from the system (Constantin et al., 2010). Using cover crops in the off-season resulted in a reduction of 36–62% of N loss from the system compared to no-cover crop in three different locations. However, the large variability in the reduction of N loss by cover crops in three different locations also indicated that other factors such as precipitation, soil types and crop rotation also affect the amount of N leaching (Constantin et al., 2010). To test the effectiveness of cover crops in reducing N loss under different cropping practices, Lemaire and Meynard (1997) investigated 6-year average annual N leaching loads among three cultivation systems. The conventional system received an appropriate amount of N fertilizer and two organic systems treated with and without animal manure. Mean N leaching loads between the three systems were not statistically significant when catch crops were grown. They concluded that the use of catch crop after the main crop had a potential role in reducing the risk of N leaching during off-season under different amount and quality of external inputs. Similar results were reported by Stopes et al. (2002) . Catch crops absorb N in the soil and store N, thus preventing N leaching. Therefore, the ability to store a large quantity of N and the turnover rate of the stored N in catch crops, may be important subjects to consider for the selection of catch crops. These studies highlight the importance of cover crops for reduction of N loss between growing seasons for both organic and conventional cultivation systems.

One of the distinctive differences of organically managed soils from conventionally managed soils is the diversity and quantity of functional microbial population (Mäder et al., 2002; Pimentel et al., 2005). Besides N-fixation, all other N-cycling processes are governed by the quality and quantity of substrate and microbial activity. Organic farming, which relies on ecosystem service, essentially has the potential to increase crop NUE through its cultivation practices (Veresoglou et al., 2012). For instance, the rapidly available fraction of SOM, particulate organic matter (POM), is 30–40% higher in organic systems than in conventional system and functional soil microbial community that decompose the POM may be more active and diverse in species and abundance (Lavelle and Spain, 2001; Marriott and Wander, 2006; Reilly et al., 2013). Microbial contribution to plant N acquisition is estimated to be 0–20% or more through N-fixing bacteria including free-living bacteria, and 0–80% through mycorrhizal symbiosis (Van Der Heijden et al., 2008). Ubiquitous soil symbiotic fungi, arbuscular mycorrhizal fungi (AMF) are able to transport N from soil to the host plant, although this does not appear to contribute to increasing plant biomass or

total plant N content (Hawkins and George, 1999; Hawkins et al., 2000). That study indicated that the hyphae of AMF uptake both inorganic (NO_3- and NH_4+) and organic (glycine and glutamic acid) N. The quantity of acquired N through AMF varied depending on AMF isolated and species, but the organically managed field had higher ability to uptake organic N than conventional (Hamilton III and Frank, 2001). A comprehensive review of the mechanism of N acquisition through AMF is elsewhere (Jin et al., 2012; Veresoglou et al., 2012). Recent studies suggest that the degree of N mineralization in mixed crop–livestock farming systems is partly controlled by C excretes from plant roots, which stimulate activities of the soil microbial community (De Nobili et al., 2001; Hamilton III and Frank, 2001). Promoted C exudates by glazed grass stimulate microbial activity, resulting in increase of soil inorganic N as well as plant N uptake (Hamilton III and Frank, 2001).

Predicting N Recovery from Soil Organic Matter

Unpredictable rate and timing of mineralization of N source (i.e. green manure, farmyard manure, compost, residual SOM) also impede synchronization of N sink and source in both conventional and organic agriculture. Organic N materials tend to release a form of plant available N in various manners depending on the materials, environment and agronomical practices. Nitrogen recovery in crops from SOM varies due to environment and characteristics of SOM (Amlinger et al., 2003; Crews and Peoples, 2005). The recovery rates from different SOM are variable and are generally <30% of the total recovery at first year of SOM incorporation and several percent in subsequent years (Amlinger et al., 2003; Crews and Peoples, 2005). Nitrogen mineralization models from various SOM provides rough estimates of SOM mineralization and may help to optimize N sink/source synchrony in both systems. The details of several proposed models are reviewed by Benbi and Richter (2002). Mineralization during crop growth has been estimated through non-linear equations using the separated or the total active SOM (Benbi and Richter, 2002). The common limitation of the N models under organic systems is that the active organic N pools are larger in size and variety than the inorganic pools, thus causing a significant error variance in the models (Tanji et al., 1979; Camargo et al., 1997). However, meta-analyses of accumulated laboratory data have proven that exponential models are useful to predict N dynamics when site-specific calibration is possible. These models, however, do not take into account the mineralization/immobilization reverse cycles occurring simultaneously in various N pools (Benbi and Richter, 2002; Dijkstra et al., 2009).

Exponential models are based on mathematical fitting techniques to predict N mineralization as a function of time (Benbi and Richter, 2002). The models consider existing N pools as separated fractions of soil N pools and estimate the total N mineralization from each fraction with different mineralization rates. Benbi and Richter (2002) suggested that multiple N fraction models provide better estimations of N mineralization. Therefore, the double-N-pool model (i.e. labile and recalcitrant SOM) would be the best to calculate parameters for N mineralization modeling compared with other N pool models (Benbi and Richter, 2002). By using data sets from several previous studies, Gilmour and Mauromoustakos (2011) found that the rate of N mineralization of labile N pool and accumulated N from labile N pool are correlated with the rate of labile N mineralization during the first week. These labile N mineralization rate and accumulated N could be estimated using total soil N, CO_2 release during first 3-day incubation, clay content in soils, soil temperature and moisture (Gilmour and Mauromoustakos, 2011). The environmental factors affecting N mineralization vary with the C/N ratio and biochemical quality of organic residue, soil moisture and temperature and the frequency of soil rewetting events (Cabrera et al., 2005); therefore, calibration and validation of the models are necessary for reliable prediction (Cabrera et al., 2005; Zhao et al., 2011).

Breeding for Integration of Physiological and Agronomic Strategies to Improve NUE

Genetic improvement to maximize NUE for target conditions

Genetic improvement in NUE through breeding relies on the availability of genetic variation and heritability of the morphological and physiological traits associated with NUE. Genetic variability in N uptake and utilization has been reported in several grain crops (Table 2) including wheat (Ortiz-Monasterio et al., 1997; Gaju et al., 2011; Swain et al., 2014), maize (Barbieri et al., 2008; Kalinova et al., 2014; Li et al., 2015), rice (Cassman et al., 1996; Sun et al., 2012) and barley (Sinebo et al., 2004; Anbessa et al., 2009). Existing variation in grain/total N concentration in different genotypes under the same amount of fertilization indicate the potential genotypic improvement of both NupE and NutE through breeding. Many of these studies did not focus on root traits. Roots are an interface where crops absorb N and are essential functional traits for synchrony of N supply and demand. Several positively correlated overlapping quantitative trait loci (QTLs) for root traits and N uptake have been reported (Table 4).

Functional root traits responsible for optimizing N uptake are key subjects to improve NUE. Since roots have multiple roles, improvement of a single trait in the root function is not likely to enhance N uptake and NUE (Lynch, 1995). Positive correlations among QTL for root traits, some physiological traits and N uptake in

Table 4. Co-localized QTL for GS or root traits and NUE-related traits in three major cereals.

Crops	Co-localized QTL	Population	N treatment	References
Wheat	Grain fill duration and plant height (4B)[1], days to anthesis (5D)	DHLs[2]	Mixed with a peat-based compost and slow-release fertilizer	Habash et al. (2007)
	Flag leaf weight, flag leaf GS[3] activity and flag leaf soluble protein (2A, 2B, 3A, 5A, 5D, 7A)			
	Peduncle at the grain fill and flag leaf GS activity (2B, 3A, 5A, 5D, 7A)			
	Flag leaf protein content and GS activity in flag leaf and in peduncle (5D)	DHLs	Optimal N fertilization	Fontaine et al. (2009)
	N uptake and root dry weight (1B)	DHLs	High N condition	An et al. (2006)
Maize	GS activity and TKS (5)	RILs[4]	Regardless of N condition	Hirel et al. (2001)
	GS activity and kernel number per plant (1)	RILs	High N condition	
	Leaf GS1 activity and remobilization from stem (1)	RILs	Low N condition	Chun et al. (2005)
	Leaf GS1 activity and remobilization from whole plant, post-anthesis N uptake (1)			
	Leaf GS1 activity and grain yield, Kernel number (1)	RILs	Regardless of N condition	
	Deep and thin root development and N uptake and N remobilization (2)	RILs	High N condition	Scharf et al. (2005)
	Number of secondary roots and N utilization efficiency (3)			
	Number of secondary roots and leaf senescence (3)			
	Root diameter and N uptake (5)			
	Root diameter and N remobilization (5)			
	GS activity and ^{15}N uptake (4)			
	GS activity and N remobilization (8)	RILs	Low N condition	
Rice	GS1 content in 9th leaf and one spikelet weight (2)	BILs[5]	Slow-release fertilizer	Obara et al. (2001)
	GS1 content in 9th leaf and spiklet number per panicle on the main stem (2)			
	GS1 content in 9th leaf and Panicle weight on the main stem (2)			
	GS1 content in 9th leaf and rates of full-discololara-tion (8)			
	GS1 content in 9th leaf and Panicle weight on the main stem (11)			
	GS1 content in 9th leaf and spiklet number per panicle on the main stem (11)			
	GS1 content in 9th leaf and rates for half-discoloration (11)			
	GS1 content in 9th leaf and rates of full-discoloaration (11)			

[1] The numbers in parentheses indicate chromosome numbers.
[2] Doubled haploid lines.
[3] Glutamine synthetase.
[4] Recombinant inbred lines.
[5] Backcross inbred lines.

maize, wheat and rice have been reported (Gallais and Hirel, 2004; An et al., 2006; Coque et al., 2008; Namai et al., 2009; Gaju et al., 2011). For instance, QTLs for NupE and root dry weight under low N conditions were reported linked in a Chinese doubled haploid wheat population (An et al., 2006). In a QTL meta-analysis, QTLs for NupE, traits of root architecture (root depth, surface area, diameter) and leaf stay-green positively coexisted in eight clusters of QTLs, while QTLs for N remobilization coincided with QTLs for leaf senescence in maize

(Coque et al., 2008). While referring to the results in the meta-analysis, the authors hypothesized that NupE and N remobilization (or NutE) are independently inherited traits, and traits associated with these two NUE sub-components may, therefore, be combined through breeding to further improve NUE (Dawson et al., 2008).

Although the final goal of breeding for both organic and conventional agriculture converges at increasing productivity through improvement of crop potential, biotic and abiotic resistance, in terms of root function

for improved NUE, breeding approaches depend on soil N levels where intended bred cultivars grow. Root traits for conventional agriculture require an early vigorous development of roots. Such roots are robust and uptake N when and as available depending on whether applied as conventional, slow-released or split fertilizer regime. In contrast, proliferation of root system and root biomass could be more important under organic or low available N conditions. Wheat breeding lines with early vigorous root branching resulted in a higher N uptake and biomass production in sandy soil where nitrate leaching and runoff are major problems (Wu et al., 1997; Liao et al., 2004, 2006). As a consequence, the final amount of N per plant was greater in these vigorous wheat lines than in conventional cultivars (Liao et al., 2006). This trait can, therefore, reduce N leaching into the environment when fertilizer is applied at seeding as a single dose. The authors also highlighted the significance of the root-branching pattern for early N uptake. The contribution of branched root system in the upper and middle soil profile (0–0.7 m) to N fertilizer recovery was greater than the deeper root system. This greater contribution was related to larger root length density at shallower soil profiles, although nitrate is soluble and easily moves into roots by mass flow in transpiration and diffusion, so that roots do not need to have a physical interface with N (Liao et al., 2006). Similar results were observed in maize in another study (Wiesler and Horst, 1994). Cultivars with this trait may be more versatile for any cultivation strategies to reduce N loss if the capacity of N storage in their vegetative parts is high.

For crops grown in limited N condition, the proliferation of roots is advantageous where there is irregular and unpredictable soil N availability. Increased proliferation of roots is considered an adaptability to the spatial and temporal heterogeneity of soil N concentration in several crops, including maize, wheat and barley in response to the localized high N availability (Drew et al., 1973; Drew and Saker, 1975; Hong-Bo et al., 2012; Jing et al., 2012; Shen et al., 2013). The proliferation of lateral roots in high N concentration patch and consequent increased N inflow into crops logically increase NUE under soil conditions of uneven SOM, which is characteristic of organic fields. The benefit of lateral root proliferation can be expected not only in organic, but also conventional fields with band placement of N fertilizer. Although there appears to be a small contribution of the root proliferation to total N uptake in some studies (Wiesler and Horst, 1994; Van Vuuren et al., 1996), the mechanism underlying this root proliferation within the soil zone of localized high N concentration has been only validated on the basis of single plant inter-C/N economy (Robinson, 2001). In the plant inter-specific competition model, the author found that the extra C required for the proliferation of roots was just 0.2% of daily C gain from photosynthesis under 12 h photoperiod, which is much less than that for establishment of AM symbiosis (e.g. 4–20%) (Douds et al., 2000; Graham, 2000; Robinson, 2001). The ability of C assimilation and allocation that is governed by the gradient of labile C in shoots and leaves is assumed to have an influence on root biomass production (Andrews et al., 2001; Chun et al., 2005). Therefore, as long as the sacrifice of C to promote root proliferation is at a reasonable cost and compensates the benefit of extra N inflow, it can be beneficial to choose any means of fertilization that promote root proliferation. The gene responsible for this reaction is well-described in a review (Walch-Liu et al., 2006a).

An investigation of the genetic relationship between the height reducing *Rht* genes and root traits using doubled-haploid and near-isogenic lines in wheat found coincidence of QTLs for plant height and root traits (Bai et al., 2013). Dwarfing genes (*Rht-B1c, Rht-D1c* and *Rht12*) reduced root-related traits, including root length, total root surface area, root dry weight and some *Rht* genes controlled both height and root traits (Bai et al., 2013). We may need to take into account this relationship between *Rht* genes and root traits because the introduction of *Rht* dwarfing genes may have a negative impact on root proliferation traits that can be useful characteristics for improving NUE (Bai et al., 2013; Hawkesford, 2014).

Walch-Liu et al. (2006b) proposed a novel theory that the presence of L-glutamate in organic N-rich soil induces shorter but branched root system in *Arabidopsis* to efficiently acquire N, while inhibiting primary root growth. They observed natural variation for L-glutamate sensitivity among different ecotypes, suggesting that this initiation of root branching is genotype-dependent. This finding suggests that breeders might take advantage of this trait to develop new cultivars with branched roots. This trait may be more advantageous for crops grown in organic fields because, in general, soil under organic management contains more SOM thus is likely to have more L-glutamate than in conventional management. Further detailed studies of genes involved in the response of L-glutamate are needed. As a result of significant interaction between genotypic profiles and soil N availability, selection for elite NUE traits adapting given N levels should take place at several levels of soil N concentrations in order to devise their potentials toward appropriate agronomic practices (Poorter and Nagel, 2000; Trachsel et al., 2013; Obara et al., 2014).

Optimization of N supply and demand

The observed genetic variation for NUE in various grain crops under different spatial and temporal soil N availability suggests a possibility to optimize NUE by filling the gaps in these environmental- and cultivar-specific variations (Scharf et al., 2005; Coque et al., 2008; Anbessa et al., 2009; Bancal, 2009; Cui et al., 2009; Gaju et al., 2011).

The breeding strategy for improved morphological and physiological N efficiency is mainly based on knowledge

of functions of crop organs and enzymatic activities involved in N metabolism of absorption, assimilation, translocation and remobilization by considering the crop itself or cereals as N sink (Fig. 1) (Simpson et al., 1982; Cormier et al., 2013). Thus, the characterization of related traits needs to be explored. Contrarily, agronomic strategies for better NUE are based on strategies that reduce N loss from soil systems and efficiently supply N according to crop demand. Although theoretical mechanisms of each NUE component have been studied for decades, improvement of a single crop trait or cultivation technique does not necessarily result in increased crop NUE (Fraisier et al., 2000; Pathak et al., 2008). Several NUE studies emphasize the importance of synchrony between N supply from N sources and plant N demand as an N sink (Sandhu et al., 2000; Crews and Peoples, 2005; Shanahan et al., 2008). Asynchronous events could happen spatially and temporally when N supply exceeds plant demands or when N supply is insufficient to meet crop demands (Crews and Peoples, 2005). Although, the former often occurs in conventional systems and the latter is more prominent in many low input/organic production systems, improvement of synchrony between N demand and supply, and reduction of N loss from agricultural systems, maybe achieved through a combination of several different approaches (Table 5). The integration of knowledge from breeding and agronomic strategies, therefore, may provide useful information to improve NUE although the lack of on-farm studies about optimization of N supply and demand will require long-term commitments.

As a result of significant interaction between genotypic profiles and soil N availability, selection for elite NUE traits should take place at several levels of soil N concentrations in order to devise appropriate agronomic practices (Poorter and Nagel, 2000; Trachsel et al., 2013; Obara et al., 2014). The scarcity of N in the soil solution results in greater biomass partitioning in roots than in shoots (Poorter and Nagel, 2000; Chun et al., 2005). In this situation, a cultivar with improved stay-green trait may not display its ability toward NUE. It has also been reported that root growth angles of maize inbred lines become steeper (i.e. deeper) in N deficit condition (Trachsel et al., 2013). The total root length in rice increases in high soil ammonium concentration (Obara et al., 2014). Through these responses to soil N concentration, crops modify their root systems. It has been demonstrated that the relative contribution of NupE and NutE on NUE depends upon the soil N levels (Moll et al., 1982; Le Gouis et al., 2000). The contribution of NupE toward NUE is greater than that of NutE in low soil N concentrations in spring wheat (Ortiz-Monasterio et al., 1997; Le Gouis et al., 2000; Muurinen et al., 2006). The contributions of both NupE and NutE are same at moderate soil N concentrations, and that of NutE is greater than NupE under high soil N levels (Ortiz-Monasterio et al., 1997). In a study of genetic variability among ancestral and modern cultivated wheat, Gorny and Garczyński (2008) found that under low soil N level, the primitive polyploid species had higher NupE, whereas the modern cultivated hexaploid species had better NutE. Generally, a low soil N level decreases biomass and grain yield, but improves NutE in wheat (Gorny and Garczyński, 2008). Therefore, selection from a wide range of germplasm under low soil N levels may be useful in breeding cultivars for different management systems (Reid et al., 2009). Although results of these studies varied, they did indicate genetic variability with differences in soil N concentration. Therefore, performance of new cultivars may not meet breeders' expectation when grown under conditions different than those where breeding was practised. In addition, heritability of NUE-related traits seems to vary with N levels, which complicates selection for these traits (Presterl et al., 2002; Laperche et al., 2006; Coque et al., 2008; Reid et al., 2009). Therefore, it is useful to have more information about the behavior of important NUE-related traits under different soil N concentration to breed ideal cultivars for specific N management practices.

The concept of N dilution curve has been studied as a crop N status indicator. This curve is a plant-based diagnostic tool providing an estimation of the crop total N requirement under given N conditions for optimum biomass production (Greenwood et al., 1990). Nitrogen concentration in crop aboveground biomass declines according to growth stages even under optimal soil N levels (Justes et al., 1994; Hoogmoed, 2015). This N dilution phenomenon is commonly shared in any species and genotypes of crops grown in any climatic conditions and is related to plant aboveground biomass production (Lemaire and Meynard, 1997; Lemaire et al., 2007). The curve is, therefore, a useful decision-making tool for N fertilization. Crop-specific nitrogen dilution curves have been proposed in wheat (Justes et al., 1994; Ziadi et al., 2010; Hoogmoed, 2015), rice (Sheehy et al., 1998; Ata-Ul-Karim et al., 2014a, b) and maize (Herrmann and Taube, 2004). Utilization of the curve to evaluate a critical point of the best balance between crop N concentration and biomass may be another approach for improving crop NUE.

Application of NUE knowledge is more challenging in organic production systems due to a number of uncontrollable biotic- and abiotic factors, which result in significant phenotypic variation. Therefore, synchronization in N sink and source in organic fields is more challenging. From sink's perspective, for instance, the prediction of expected genetic gain in spring wheat by direct selection in an organic field is difficult because genetic parameters cannot be precisely estimated due to variability in some agronomic traits (Reid et al., 2009). A low heritability for grain protein content is reported in organically grown wheat, while others reported high heritability for NupE, NutE and NrE in wheat and maize under organic conditions (Presterl et al., 2002; Coque and

Table 5. Factors controlling synchrony between nitrogen supply and crop demand in conventional and organic agriculture (Crews and Peoples, 2005).

Variables	Interaction with N	Strategies	Consideration	N source/sink
Crop	• Absorption of N • N storage in biomass	• Improvement of (1) the total crop N demand; (2) root function to absorb existing N; (3) N metabolisms to develop grain • Monitoring crop N status to optimize fertilization • Diversification of crop cultivars and species	• The amount and timing of N requirement in growth stage • Crop yield response to the amount of applied N • Growing season	N source/sink
Fertilizer	• Supplementation of N in soils • N loss in environment	• Choice and timing of N fertilization according to crop N demand (e.g. manure, compost, split-application, top-dressing and slow-releasing) • Soil N analysis before seeding • 4R practice	• Behavior of mineral N • Cost and return of application	N source
Tillage	• Promotion (tillage)/depression (no-till) of SOM decomposition • Weed (N pool) management	• Increased aeration to promote decomposition of SOM where N supply is limited (e.g. organic agriculture) • Reducing tillage practice to increase SOM accumulation to maintain a capacity of soil to prevent N loss from systems	• Proper type and timing of tillage practices	
Crop choice	• Absorption of N • N storage in biomass	• Increased SOM and N storage capacity	• Biomass production • C/N ratio	N source/sink
Water management	• Movement of labile N in systems	• Monitoring and assessing N loss due to water movement	• Rainfed or irrigated	
Biological N-fixation	• Contribution to providing N to plants and systems	• Incorporation of leguminous plants in rotations • Inoculation of legumes	• Crop and rhizobia interaction • Antagonism between inorganic fertilizer and efficiency of N-fixation by rhizobia	N source
Soil microorganisms	• Control of decomposition and mineralization • Enhancement of crop N absorption	• Maintaining a favorable environment for diverse soil microbial communities • Refrain from excessive use of synthetic fertilizer, fungicide and pesticide	• The rate of decomposition, mineralization, immobilization, volatilization, ammonification and denitrification • Carbon source for respiration and growth	N source/sink
Other agricultural practices	• Prevention of erosion, runoff and leaching • N storage in biomass	• Incorporating several different practices (e.g. crop rotation, cover cropping, relay cropping, alley cropping and catch cropping) to reduce N loss from systems • Utilization of decision-making tools (e.g. N dynamics prediction and crop N requirement prediction) • Precision N fertilization	• The quality of cover cropping, relay cropping as temporary N storage and N source to be decomposed • Cost and application of advanced technologies	
Soil property, characteristics	• A temporal (short and long terms) N storage	• Amending factors that restrict plant root growth • Amending soil pH, moisture, aeration • Remote sensing of soil N dynamics	• Physical, chemical and biological properties that affect N dynamics for short and long-term perspectives	N source/sink
Climate	• Affecting N loss, SOM decomposition and crop development	• Referring to a local weather forecast (e.g. temperature and precipitation)	• Rainy season, annual temperature, growing degree days	

Gallais, 2007; Reid et al., 2009). Struik and Yin (2009) concluded that polygenic control, environmental variation (e.g. plant available N concentration, timing and amount of mineralization, weed and disease pressure) and their interaction with NUE-related traits cause inconsistencies and hinder improvement of crop NUE through conventional breeding. Therefore, QTL mapping and marker-assisted selection for traits associated with NUE and the interaction of these genes/QTLs with environment and management practices may provide breeders with tools to improve NUE for target management systems (Struik and Yin, 2009; Van Bueren et al., 2010).

Conclusion

NUE is a complex trait to improve with many potential interactions and trade-offs with other factors controlling final yield. Key genotypic factors for improving crop NUE seem to be common traits between conventional and organic agriculture. Those traits capture and utilize N when it is available for grain production. However, those regulations and responses vary according to genotypes, environmental and agronomic regimes. Therefore, a genetic, environmental and N-level interaction should be taken into consideration in breeding programs for intended production systems. The agronomic approach requires considering ways to synchronize N supply with crop N demand besides optimizing N utilization in a system. Implementation of BMPs for N fertilization has great potential to fill the gap between optimum and the actual current practices, and thus in the improvement of NUE in conventional production systems. Organic practices put more emphasis on incorporation of legumes in crop rotation and diversification of cropping practices. Factors controlling crop NUE and the efficiency in crop production management are intertwined in both organic and conventional systems. The challenge of maintaining crop yield and improving NUE needs emphasis globally. While theoretical approaches to improving NUE by altering single traits related to N efficiency are necessary, studies covering holistic approaches will lead to improvement of NUE within the entire agroecosystem.

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