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Review

Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems

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Abstract

Low-input and organic farming systems have notable differences in nitrogen (N) sources, cycling and management strategies compared to conventional systems with high inputs of synthetic N fertilizer. In low-input and organic systems, there is greater reliance on complex rotations including annual and perennial crops, organic N sources, and internal N cycling that more closely mimic natural systems. These differences in farming system practices fundamentally affect N availability and N use efficiency (NUE) and could impact crop traits and breeding strategies required to optimize NUE. We assess genetic and environmental factors that could assist breeders in improving crop performance in low-input and organic farming systems by examining NUE in natural and agricultural ecosystems. Crop plants have often been bred for high N productivity, while plants adapted to low N ecosystems often have lower productivity and higher levels of internal N conservation. Breeders can potentially combine N productivity and N conservation through the use of elite and wild germplasm. Beneficial genetic traits include the ability to maintain photosynthesis and N uptake under N stress and the ability to extract soil N at low concentrations, perhaps through beneficial associations with soil microorganisms. In addition, breeding for specific adaptation to climactic and management practices so that crop uptake patterns match N availability patterns, while minimizing pathways of N loss, will be critical to improving NUE.

Keywords: Nutrient cycling; Perennial crops; Cereal crops

Contents

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1. Introduction

In the initial stages of crop domestication, plants were still subject to many of the same natural selection pressures as their wild progenitors. Environmental heterogeneity and unpredictability were characteristic of these early agricultural systems. Over time, agriculture evolved to overcome production risks associated with environmental variability by developing mechanical, genetic and chemical means to reduce variability and improve crop performance. Today, many agricultural breeding programs are conducted in environments where inputs such as nitrogen (N) fertilizers are highly regulated to ensure that crop deficiencies are minimized. In contrast, low-input and organic farming systems often have limited pools of mineral N and a greater reliance on organic sources and internal cycling of N. Consequently, traits related to nitrogen use efficiency (NUE) in an evolutionary context may be more important for low-input and organic systems than in conventional systems.

Despite its importance, a clear understanding of the major mechanisms and inheritance of NUE is lacking (Basra and Goyal, 2002). Part of this is due to the inherent complexity of NUE, as it is a function of multiple interacting genetic and environmental factors. Disagreements often arise not only in partitioning variation to genetic or environmental causes, but in the definition of NUE itself. Nevertheless, the first stage in many breeding projects is to define the desired phenotype and important traits which can contribute to improvements in NUE.

Genetic mechanisms of agricultural NUE have primarily been studied in conventional systems where traits under selection are often directed toward increasing the response of crop yield and quality to applied N; subject to the law of diminishing returns (Spillman and Lang, 1924). While these systems can create N stress, they do not capture the range of environmental and management factors present in low-input agricultural systems. Here, the range and complexity of environmental stress and interacting genetic components are more similar to less regulated natural ecosystems. Key components of NUE in natural ecosystems relevant to improving NUE in low-input and organic farming systems likely include N conservation, internal N cycling and adaptation to low N conditions. Less is known about the genetic factors controlling N use efficiency in such systems, and whether the genetic mechanisms differ significantly between high and low fertility environments. Therefore, studies on the NUE of plants and populations in natural ecosystems could aid in designing selection regimes and identifying specific traits that are useful for improving varietal performance in low-input and organic systems.

The most immediate goal of improving agricultural NUE is to improve the recovery of N from fertilizer, either organic or synthetic. Globally, only a third of the N in fertilizer applied to cereal crops is harvested in the grain (Raun and Johnson, 1999). Future costs of N fertilizer will increase as natural gas becomes scarcer. Currently, one metric tonne of fertilizer N synthesized through the Haber–Bosch process requires 873 m^3, or 35 million British Thermal Units (BTU), of natural gas (Vance, 2001). In addition, transporting and applying such fertilizers takes fuel energy and labor. Many farmers want to minimize costs associated with N fertilizers as well as potential adverse impacts on water, air and soil quality.

Several different strategies are currently being pursued to address problems associated with inefficient agricultural systems and the N cascade (Galloway et al., 2002). Precision N management can improve NUE by tailoring applications of fertilizer N to site-specific conditions in order to reduce N losses and optimize crop performance. Breeding efforts are aimed at developing crop varieties that are more efficient at capturing soil N, thereby decreasing N leaching and denitrification losses and reducing plant N requirements (Cassman et al., 2002). Genetic studies with small grains have been primarily concerned with improving NUE as a means of increasing grain protein content and yield response to applied N fertilizer. While this can also reduce the N requirement of plants for a given yield and protein goal, it does not directly address the environmental impacts of excess N fertilization. The most comprehensive solution is to redesign the cropping system making use of management tools such as rotations, mixtures, and perennial crops. This approach requires the most drastic change but may be necessary when considering agricultural sustainability over a longer timeframe. Many organic and low-input farms use an integrated approach to maximize on-farm nutrient cycling and to build or maintain soil fertility and crop productivity. These systems could benefit from both site-specific N management and crops bred for improved NUE without synthetic N applications.

Breeding crops specifically for organic and low-input systems is gaining attention as farmers and researchers realize that beneficial traits for these systems may be very different from those that produce high yields in conventional systems (Murphy et al., 2007). Since N is a major limiting factor in low-input and organic cereal production, the development of highly efficient varieties could hasten the adoption of these systems and also make it possible to reduce levels of N fertilization in conventional agriculture. Our objectives are to: (1) integrate ecological and agricultural concepts and definitions of NUE; and (2) discuss strategies for breeding grain crops with higher NUE in organic and low-input farming systems.

2. Nitrogen use efficiency: concepts and definitions

2.1. NUE of annual grains

Moll et al. (1982) defined NUE as the ratio of grain weight to N supply (G_w/N_s) and N supply as the amount of plant available N in the soil. The authors noted that plant available N

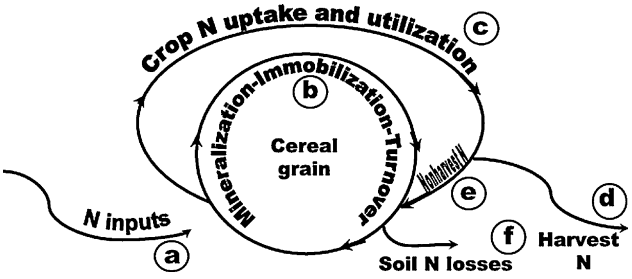

Fig. 1. Pathways affecting nitrogen use efficiency in cereal cropping systems. Circled letters refer to letters in parentheses in Table 1. (After Huggins and Pan, 2003).

was difficult to measure and that many researchers substitute applied fertilizer N when calculating NUE. Because all applied fertilizer N is not available to the plant and applied fertilizer N is not the only source of available N, this definition does not provide a complete picture of NUE. This is particularly the case with low-input and organic systems where inputs of synthetic N fertilizers are minimized or absent. Huggins (1993) adapted the formula of Moll et al. (1982) to aid partitioning between soil and plant physiological process and effects. They redefined N supply as the amount of N potentially available to plants including N losses and immobilization and added the term Nav to represent plant available N. Plant available N was defined as the difference between N supply and N losses associated with leaching, volatilization, runoff, denitrification and immobilization (see Fig. 1, Tables 1 and 2 for a summary of NUE components).

The ratio of plant available N to N supply is the system N retention efficiency (N_{av}/N_s), or the proportion of the N supply that is available to plants that season. While N retention

Table 1
Components of nitrogen use efficiency for annual crops

Component symbol and descriptor		Example
G_w	Grain dry weight	4394 kg ha^{-1}
H_w	Harvested biomass dry weight	4904 kg ha^{-1}
N_s	N supply	229 kg N ha^{-1}
N_t	Total N in plant	128 kg N ha^{-1}
N_g	N in grain	104 kg N ha^{-1}
N_{av}	Plant available N	155 N kg ha^{-1}
G_w/N_s	N use efficiency	19.2 (a, b, c, e, f)
N_t/N_s	N uptake efficiency	0.56 (a, b, c)
G_w/N_{av}	Plant available NUE	28.3 (a, b, c, f)
N_{av}/N_s	N retention efficiency	0.68 (a, b, f)
G_w/N_t	N utilization efficiency	34.3 (c)
N_t/N_{av}	Available N uptake efficiency	0.83 (a, b, c, f)
N_g/N_s	Grain N accumulation efficiency	0.45 9 (a, b, c, d)
N_g/N_t	N harvest index	0.81 (c, d)
N_c/N_t	N carry-over efficiency	n.a.
H_w/N_s	Forage NUE, definition 1	21.4 (a, b, c, e, f)
H_w/N_t	Forage NUE, definition 2	38.3 (c)

After Berendse and Aerts (1987) and Huggins and Pan (2003). The example values are for annual wheat, from Huggins (1993). Measurements given in the upper part of the table are used to obtain the example values in the second part of the table. Letters in parentheses refer to pathways in Fig. 1 that impact the component of NUE being calculated.

Table 2
Components of nitrogen use efficiency for perennial species

Component symbol and descriptor	
$MRT \times A$	N use efficiency
L_n	relative N requirement
MRT	mean residence time, in days, L_n^{-1}
A	N productivity, g^{-1} N day^{-1}

After Berendse and Aerts (1987).

efficiency primarily relates to soil N cycling and flow, it is also related and in part due to plant N uptake. If plants have higher N uptake, there is less soluble N in the soil that could be immobilized or lost (Fiez et al., 1995). This recognizes the complex interaction between plant and soil to determine N availability and uptake. In field experiments, plant available N may be calculated as the total N in plant tissues plus the residual inorganic soil N within the root zone. Using the calculated value of plant available N, it is possible to obtain the plant available NUE (G_w/N_{av}). This is the same as NUE (G_w/N_s) if there are no N losses. Plant available NUE is a measure of efficiency for the plant, whereas the original formula looks at the NUE of the system, without separating plant and soil influences.

It is also possible to measure the grain N accumulation efficiency (GNACE), which is the amount of N in the grain divided by the N supply (N_g/N_s). It serves as a measure of the overall efficiency with which plants extract N from the soil and accumulate it in the grain by harvest. An additional important parameter is the N harvest index (NHI). NHI is the ratio of N present in grain to total plant N content (N_g/N_t), analogous to the harvest index (HI), which is the ratio of grain to total biomass. It is a measure of N translocation efficiency. Although not directly related to grain weight, it has significance for maximizing grain protein content for a given amount of plant N.

Two plant physiological components, N uptake efficiency and N utilization efficiency, contribute to overall NUE. N utilization efficiency (G_w/N_t) measures the response of grain yield to the total N in the plant. Since total plant N is difficult to measure, most experiments measure aboveground plant N, ignoring the root system. This may not be significant when comparing genotypes that have similar root systems, however, it may be important if comparing plants with different root architecture and biomass. As with the substitution of N fertilizer for N supply, this does not change standard calculation methods but must be acknowledged as a factor when interpreting results. It must also be remembered that NHI, GNACE and N utilization efficiency do not account for potential volatilization losses during translocation. Volatilization is difficult to quantify and reduces total plant N measured at harvest, so if volatilization losses are significant, plants may seem to have greater efficiencies than is actually the case.

N uptake efficiency was defined by Moll et al. (1982) as total aboveground plant N at harvest divided by the total N supply (N_t/N_s). Huggins and Pan (2003) modified this to improve the accuracy of measuring plant efficiency, by accounting for potential losses and calculating plant available N uptake efficiency (N_t/N_{av}). Uptake efficiency is a measure of how much N the plant absorbs in proportion to the N supply (or plant

available N). Plant uptake is closely associated with assimilation, the incorporation of N compounds into plant tissues. Many authors who use the older formula (N_t/N_s) find that uptake efficiency decreases with increasing N supply. Huggins and Pan (2003) found that decreasing efficiency at higher N supply was not mainly due to decreased plant uptake but was mostly because of greater losses from the system. Not accounting for N losses could therefore be misleading when analyzing plant N uptake efficiency.

The definition and components of NUE in annual grains place an emphasis on grain yield and protein. While these two traits are extremely important in agriculture, the definition of NUE as the ratio of grain yield to N supply measures the plant response to available N rather than the efficiency of the system as a whole. In more diverse rotational systems, the NUE of the system over time and the ability to minimize N losses may be just as important as the yield response to N in any particular year. For these systems, studies on the NUE of perennial species in natural ecosystems and pastures is very relevant. From an ecological point of view, the response to available N is not as important as the long-term survival and N balance of populations.

2.2. NUE in natural ecosystems and perennial species

Berendse and Aerts (1987) discussed previous attempts to define NUE in biologically meaningful ways for natural ecosystems and proposed a new definition that could be useful for assessing adaptation to habitats with different N regimes. They stated that NUE should include two components: (1) the mean residence time (MRT; day) of N in the plant; and (2) the rate of biomass production per unit of plant N (A; g dry biomass g^{-1} N day^{-1}). They defined NUE as the product of MRT and A; the amount of biomass that can be produced per unit of N obtained by the plant (g dry biomass g^{-1} N). The MRT is the average length of time a molecule of N remains in living plant tissue and is dependent on the rate of N loss from the plant through volatilization, root exudation, herbivory and tissue senescence. Species with a long MRT (low N loss rate) would be favored in environments with poor N supply, whereas species with high A would be favored in comparatively N-rich environments. This definition of NUE has also been applied to perennial forages (Vazquez de Aldana and Berendse, 1997). Forage NUE, however, is often measured as the amount of forage dry matter produced per unit of applied N (Zemenchik and Albrecht, 2002). This is analogous to the measurement of grain yield per unit of applied N in annual cereals, but as previously discussed does not account for N losses and immobilization, or the availability of N from other sources.

2.3. Unifying definitions of NUE

While the terminology is different, there are clear similarities between the definition of NUE in agricultural systems and that in natural ecosystems. Both measure biomass produced per unit N, although in natural ecosystems the emphasis is on total biomass, whereas in agricultural systems the harvested biomass (grain or forage yield) is a major consideration. In annual cropping systems, NUE calculations are largely based on measurements at harvest as this is the end of the plant's life-cycle. However, calculating NUE at a single point in time rather than at several different growth stages may not give a complete picture of the N dynamics of the crop over the growing season. If certain varieties have lower levels of N loss, they may be able to produce biomass with less total N over their lifecycle than varieties that have more rapid N turnover, even if they have equivalent yield and N concentration at harvest.

In natural and agricultural systems with biannual and perennial species, biomass production and internal plant N turnover over multiple seasons becomes an increasingly important factor of NUE. The yearly carry-over of N in roots, crowns and other living tissues of perennial species constitute N utilization directed toward important post-harvest physiological functions such as plant re-growth and winter survival.

Therefore, in addition to N utilization efficiencies of annual crops that evaluate harvested biomass (G_w/N_t) and N (N_g/N_t), we propose to add N utilization efficiency components that assess plant N carry-over (N_c) into the next season by biannual or perennial species. Here, N_c is defined as the amount of plant N in living tissues at harvest which along with N in non-living tissue (straw, roots) and N in the grain (N_g) comprises total plant N (N_t). The N carry-over efficiency can then be defined as N_c/N_t and the contribution of N_c toward N utilization efficiency (G_w/N_t or H_w/N_t, where H_w is the dry weight of any biomass that is harvested) can be expressed as two components: $(H_w/N_c)(N_c/N_t)$. Similarly, the NHI (N_g/N_t) can be partitioned into meaningful components where NHI= $(N_g/N_c)(N_c/N_t)$. Here, N_g/N_c is an N partitioning component related to reproductive and survival strategies of the plant where N resources are allocated to protein synthesis in seeds and/or to physiologically active non-reproductive tissues such as leaves, crowns and roots.

The inclusion of N_c in the evaluation of NUE uses a mass balance approach to address issues raised by N MRT. But rather than assuming a steady-state condition in plant (or population) N retention has been reached to enable the calculation of MRT, critical time periods as defined by key physiological or management criteria allow NUE assessment to be linked to the dynamics of system N cycling and flow. Consequently, although harvest is often a critical time period for evaluating NUE, other physiologically important stages may be identified and used as selection criteria in a breeding program or to evaluate different N management strategies. Evaluating key NUE components at strategic times and integrating this information over the course of a crop sequence or rotation can provide the basis for assessing NUE over a wide variety of agricultural systems using the same definitions and framework.

3. Genetic and environmental variation in NUE

Previous studies have extensively characterized crop performance (e.g. yield, quality, NUE) under various fertilizer and management regimes in different environments. Results are commonly inconsistent and disagreements arise when partitioning variation in crop performance to genetic or environ-

mental factors. Conflicting results could be due to differing research methods, management practices, climate, genetic materials, and definitions of NUE (Huggins and Pan, 2003; Van Sanford and MacKown, 1987). For example, studies involving a narrow subset of elite genetic material are less likely to find significant genotypic variation for NUE than studies that sample a diverse group of modern and historic varieties. In addition, soil N supply, total plant N, harvested N and N lost from the system are variables that are temporally and spatially dynamic and difficult to accurately measure, therefore making comparisons among studies in different environments problematic (Fowler et al., 1990).

Despite the variation in crop performance arising from genetics, environment and their interaction, studies of forages and annual grains over a wide range of N supply show that agricultural NUE increases as N fertility decreases (Dhugga and Waines, 1989; Gauer et al., 1992; Huggins, 1991, 1993; Huggins and Pan, 2003; Jiang and Hull, 1998; Jiang et al., 2000; Oritz-Monasterio et al., 1997; Singh and Arora, 2001; Vazquez de Aldana and Berendse, 1997; Zemenchik and Albrecht, 2002). Reductions in NUE with increasing N supply could result from reductions in any of the components, including N-uptake efficiency, N utilization efficiency and N retention efficiency. Studies on wheat and perennial grasses have shown reductions in all of these components (Cox et al., 1986; Dhugga and Waines, 1989; Huggins and Pan, 2003; Jiang et al., 2000; Morris and Paulsen, 1985; Oritz-Monasterio et al., 1997). For example, Oritz-Monasterio et al. (1997) found that in all varieties evaluated, both uptake and translocation/utilization efficiency were reduced at higher N supplies, causing an overall reduction in NUE. Morris and Paulsen (1985) and Cox et al. (1986) showed a reduction in translocation efficiency at high N compared with low N supplies. Dhugga and Waines (1989) attributed decreased NUE at high N to higher volatilization losses because the plant was unable to assimilate all the N taken up. Huggins and Pan (2003), in contrast, found that there actually was a slight increase in available N uptake at higher N levels, but there was a severe decrease in soil N retention efficiency which resulted in a net reduction in NUE.

Studies examining post-anthesis N nutrition of wheat in order to enhance grain protein provide an interesting example of the interactive effects of genetics and environment. Many farmers increase the rate of N fertilization to meet grain protein concentration targets when growing high-yielding varieties of wheat. Available N early in the season generally contributes to increasing vegetative growth and establishing the reproductive sink capacity, which determines the maximum possible yield. However, excessive vegetative growth can use up available soil water in drier areas and restrict grain production later in the season (Halvorson et al., 2004). Applying high rates of synthetic N at early growth stages may lead to high losses since plant demand is initially low. Loss of N from available pools, however, is dependent on the strength of competing N pathways including leaching, volatilization and immobilization from the time of application to N uptake. Consequently, synchronization of N application with crop N demand may not lead to greater NUE, rather it is the synchronization of N availability with plant N demand and uptake coupled with the lack of synchronization of available N with competing N pathways that promotes greater NUE. Post-anthesis N fertilization of wheat can provide N for grain protein accumulation, but may not be effective if foliar N uptake is limited, insufficient soil moisture restricts root uptake, or competing N loss pathways reduce N availability (Cox et al., 1985a; Harper et al., 1987; Soon, 1988). Lack of available N uptake due to environmental or physiologic constraints can occur even when the sink strength for grain protein synthesis is high, resulting in N losses and low NUE.

Plants with more extensive root systems may be able to reach moisture and N stored lower in the soil profile. Cox et al. (1985a) found a significant negative relationship between N assimilation after anthesis and total aboveground dry matter at anthesis and attributed some of this variation to certain genotypes having larger root systems or root systems that used soil N more efficiently. Their interpretation was that lines with high aboveground biomass at anthesis probably had less biomass belowground in roots, and were not able to take up N later in the growing season at lower concentrations and greater depths in the soil. McKendry et al. (1995) found that the two best varieties for NUE were better able to survive extreme drought, suggesting more extensive root systems. Similarly, in perennial grasses grown under drought conditions, species and varieties with more extensive root systems had greater N uptake (Jiang et al., 2000; Zemenchik and Albrecht, 2002).

Organic and low-input systems usually have very different seasonal N cycling and availability than conventional systems that use synthetic fertilizers. Reliance on organic N sources requires an understanding of organic N mineralization–immobilization and turnover (MIT) patterns in relation to crop N demands and N loss pathways. MIT is stimulated by temperature and water conditions that often favor plant growth and biological regulation of N availability and assimilation by plants can be augmented in these systems. For example, the use of perennial species and more diverse crop rotations can increase the temporal and spatial regime of active root systems, thereby limiting N losses and increasing NUE (Collins and Allinson, 2004).

Studies on NUE in annual wheat have established that significant genetic variation exists for traits related to NUE (Dubois and Fossati, 1981; Fowler et al., 1990; Loffler and Busch, 1982; May et al., 1991; Paccaud et al., 1985; Singh and Arora, 2001; Van Sanford and MacKown, 1986). In addition, the heritability of these traits is high (Agrama et al., 1999; Coque and Gallais, 2006; Cox et al., 1985b; Davis et al., 1961; Fowler et al., 1990; Loffler and Busch, 1982; Presterl et al., 2002). In wheat, significant genetic variation exists for total N uptake (McKendry et al., 1995) and for translocation efficiency (Cox et al., 1986; Johnson et al., 1968). Genetic variability for post-anthesis N uptake has also been reported (Austin et al., 1977; Clarke et al., 1990; Neales et al., 1963). N uptake and N remobilization also appear to be independently inherited traits so favorable alleles could be combined when breeding for NUE (Johnson et al., 1967; McKendry et al., 1995; Presterl et al., 2002; Sattlemacher et al., 1994). In Kentucky bluegrass, a

perennial species, there are significant differences between varieties for N uptake and NUE (Jiang and Hull, 1998; Wilkins et al., 1999). The presence of genetic variation for traits that contribute to NUE suggests that breeding for improved NUE in low-input and organic systems is possible.

It would be useful to have more information on the relative importance of many traits related to improved NUE, however, the environmental context and the particular genotypes grown appear to have a large effect on research findings. The genotype by environment (G × E) interaction may have a larger effect on NUE than the genotypic contribution itself (Bertin and Gallais, 2000). High levels of G × E interaction mean that it is important to conduct research in the target system, whether the goal is to understand factors that contribute to NUE in that system or to breed varieties with high NUE. This is especially important in low-input and organic systems which are characterized by environmental heterogeneity and which cannot be made uniform through the addition of fertilizer N.

4. Ecological effects of N limitation

The efficient use of N should be favored by natural selection, and may have been under significant selection pressure during the domestication and evolution of crop species. Directional selection, whether natural or artificial, is expected to reduce the amount of genetic variation present in populations (Ackerly et al., 2000; Byers, 2005). However, environmental heterogeneity over time or space could lead to the maintenance of genetic variation at loci that contribute to NUE. Environmental unpredictability can lead to selection for phenotypic plasticity and the ability for plants to produce more than one phenotype depending on the environmental conditions (Byers, 2005; Górny, 2001).

NUE in terms of evolutionary fitness is different from NUE in an agricultural setting. In natural ecosystems, inorganic N pools are often extremely limited, and natural selection may work to maximize the conservation of N within plant tissues rather than the maximum biomass production per unit N (Silla and Escudero, 2004; Vazquez de Aldana and Berendse, 1997). There appears to be an ecological trade-off between N productivity and MRT. In fertile environments, a high relative growth rate gives species an advantage, but also means higher rates of nutrient turnover and loss from plant tissues (Aerts and van der Peijl, 1993; Berendse and Aerts, 1987). In low N environments, species with a high growth rate will produce more biomass in the short term, but will have lower productive potential after a few seasons compared to species adapted to low N environments which have a longer MRT and lower rates of N loss (Aerts and van der Peijl, 1993). Early successional species, often annuals, may have an advantage when colonizing new areas because of their rapid growth rate, but then are displaced by species with slower growth rates and better internal N conservation (Tilman, 1986).

Adaptation to low N environments includes a higher root to shoot ratio and a lower relative growth rate. Greater root biomass and mycorrhizal connections are more important than a rapid absorption capacity since mass flow and diffusion through the soil limits the rate at which N is available (Chapin, 1980). Because root absorption rates are proportional to efflux rates, reducing the absorption rate also limits nutrient loss. Species adapted to fertile environments have higher rates of fine root turnover, which increases the absorption capacity per unit of root length, but also increases nutrient loss because resorption of N from senescing roots is minimal (Silla and Escudero, 2004). Species adapted to low N conditions are able to take up more N at low concentrations than those adapted to high N conditions and vice-versa (Chapin, 1980; Jiang and Hull, 1998). In a study of perennial grass species adapted to, or bred for, different environments, species adapted to environments with nutrient limitations had low internal N turnover, and low biomass production per unit N. Species bred for nutrient rich habitats, such as pasture grasses, had high internal N turnover in both low and high fertility treatments and had high biomass production under high N conditions, but produced significantly less biomass in low-fertility soils (Vazquez de Aldana and Berendse, 1997). Since most crop plants were selected in, and for, nutrient rich environments, genes from native grasses or other wild relatives adapted to low N environments may be useful sources of genes for increasing N uptake and NUE in nutrient limited environments.

In perennials, N stress leads to lower rates of leaf turnover, higher root biomass, fewer tillers and less resource allocation to reproduction. This is in contrast to annuals that put all their resources into reproduction when faced with high stress levels (Chapin, 1980). Species with rapid growth rates usually have high leaf N concentrations and photosynthetic capacity, but shorter leaf life span (Silla and Escudero, 2004). Under nutrient limited conditions, slower growing species have a greater ability to maintain higher leaf N concentrations for photosynthesis (Chapin, 1980). This is because when N becomes available, plants take up more than is necessary to support the biomass they produce, often called luxury consumption. This extra N is then used for later growth, rather than being put into a flush of biomass production that can lead to plant N stress under subsequent conditions of N limitation (Chapin, 1980). This is the reverse of what would be expected in an agricultural setting, where biomass and yield response to added N is a key selection criteria, and luxury consumption to increase grain protein is achieved through adding more N than is necessary for maximum yield.

5. Management effects on nitrogen use efficiency

5.1. Nitrogen from plant sources

Organic systems differ from conventional systems in many ways, including the use of biological mechanisms of fertility and pest control and the inclusion of diverse rotations to balance on-farm nutrient cycling. There have been many studies on the role of green manures and cover crops in providing and retaining N in organic systems. In conventional systems, wheat yields are often higher following legumes than following another cereal (Dalal et al., 1998; Huggins, 1991; Soon et al., 2001; Stopes et al., 1996; Strong et al., 1986;

Weston et al., 2002), and the N uptake of a wheat crop is greater following legumes than that of wheat following wheat or fallow (Badaruddin and Meyer, 1994; Campbell et al., 1990; Huggins, 1991; Soon et al., 2001). Grain protein content and concentration is also greater following a legume crop (Badaruddin and Meyer, 1994; Biederbeck et al., 1996; Campbell et al., 1990; Strong et al., 1986). There are several reasons why rotations may improve the N dynamics of agricultural systems. Huggins (1991) attributed the increase in wheat yields after Austrian winter pea either to the peas supplying greater N for plant uptake or increasing the N uptake efficiency of the wheat crop. A break crop can also reduce the incidence of soil-borne cereal diseases. Controlling diseases leads to more vigorous plants, which may increase N uptake efficiencies because of healthier roots and greater density of root hairs (Cook et al., 1987).

Crop rotations are a fundamental component of organic systems, and legume crops are often planted to enhance nutrient cycling and availability to other crops in the rotation. Crops with high N demands are usually grown after a green manure or legume crop. Although there is some rotational benefit from grain legumes, it is unlikely that much N is provided to the subsequent crop. Dry beans harvested for grain may fix up to 200 kg N $ha^{-1}yr^{-1}$but most of this is removed at harvest. Grain legumes do conserve soil N by fixing atmospheric N, thereby leaving residual N in place for the next crop (Soon et al., 2001). However, only 50% of the total N in grain legumes is from biological fixation, in comparison to up to 80% in forage legumes (Watson et al., 2002).

The inclusion of a legume crop decreases reliance on external fertilizer if the legume crop supplies a significant proportion of the N for the next crop. Cover crops or green manures not harvested for grain are more effective than grain legumes at providing N to the subsequent crop. Soon et al. (2001) found that more N is mineralized from cover crop residues than from wheat or field pea residues. In a study comparing different legumes in rotation with wheat, only rotations that included a legume green manure crop had a positive N balance during two cycles of the rotation (Soon and Clayton, 2003). Another UK study showed that winter wheat yields were greater after legume green manures than after trefoil or ryegrass green manures, and that only the wheat following clover green manures had high enough grain protein for bread flour (Stopes et al., 1996).

In areas of high rainfall, legume green manures can produce more soluble N than the subsequent cereal crop is capable of taking up during its early growth period, increasing the risk of leaching. A pea green manure in the UK provided 335 kg N ha^{-1}, but only 13.3 kg N ha^{-1} was recovered in the following winter barley crop, probably due to low release rates from the incorporated plant material. The authors estimated that denitrification and leaching losses were small, but may have contributed to the poor crop N recovery (Redman et al., 1989). A study in Sweden with different pasture compositions and management found that green manure crops, particularly clovers, contributed much more N to the system than pastures mowed for forage production (Torstensson, 1998). Green manure treatments contained 170 kg N ha^{-1}, which was almost three times the N in mowed plots. In comparison, there were only 28 kg N ha^{-1} in barley residues. A study in Scotland had similar results, with a white clover green manure providing the highest levels of nitrate to the subsequent crop (Baggs et al., 2000). Mixed clovers and grasses fixed up to 250 kg N ha^{-1} each year, depending on the percentage of clover in the planting (Baggs et al., 2000).

In dry areas, studies have found substantially less net N mineralization than areas with higher rainfall and warmer temperatures. A study in Saskatchewan, Canada, found an average net mineralization of 18 kg N ha^{-1} for four different green manures tested in a wheat-based cropping system, with the highest being 38 kg N ha^{-1} for chickling vetch and black lentil (Biederbeck et al., 1996). In Queensland, Australia, an annual medic green manure provided from 10 to over 30 kg N ha^{-1} mineralizable N to the following wheat crop, but wheat yields following medic were still higher than those of continuous wheat with 50 kg N ha^{-1} synthetic fertilizer (Watson et al., 2002). In Northern Idaho, pea green manure provided 94 kg N ha^{-1}, while harvested seed peas provided 86 kg N ha^{-1} and summer fallow provided 73 kg N ha^{-1} fertilizer N equivalent, calculated based the difference in yield between wheat grown after the legume or fallow and that of wheat following spring barley. Yield of a winter wheat crop following the pea green manure was similar to that of wheat following fallow, but in the fallowed soil, organic matter was lost to mineralization (Mahler and Auld, 1989).

Cover crops are often grown to minimize leaching and soil erosion over winter and are taken out before planting a spring crop. Subsequent mineralization can provide N to the next crop, but synchronizing the release of N from residues with the periods of strong crop demand is difficult. Mineralization of N from legume residues may match wheat N demand fairly well, increasing uptake and decreasing the potential for leaching (Badaruddin and Meyer, 1994; Campbell et al., 1990). Rotations appear to improve N availability and uptake, and lower residual soil nitrate concentrations have been reported in wheat following legumes than continuous wheat (Soon and Clayton, 2003; Soon et al., 2001). Non-legume green manure crops can also increase system NUE, primarily by immobilizing N to limit over winter leaching followed by mineralization of this N and use by the crop after the green manure (Watson et al., 2002). Other studies, however, have shown that green manures can result in excess N which is subsequently lost, or can immobilize soil N, reducing its availability during the growing season. Kramer et al. (2002) found that N from vetch residues did not become available until 70 days after planting a maize crop. In comparison with conventional fertilizer, vetch N was released and taken up at a more constant rate over the season, while conventional fertilizer N was more available at the beginning of the season, but decreased in availability as the season went on. Despite differences in timing, however, there was no difference in crop N uptake efficiency (calculated as total aboveground plant N/N applied) between the conventional and low-input (vetch) N sources.

The C:N ratio of residues has a large effect on decomposition and mineralization rates. Most legume residues have

relatively low C:N ratios, generally between 12 and 25 (Torstensson, 1998). In contrast, cereal residues may have a C:N ratio of 80 or more, which can lead to net immobilization of N for months or years after incorporation. In general, there is no net mineralization in the first season from residues with a C:N ratio greater than 25. Incorporation of wheat residues will most likely reduce the amount of immediately available N, but will increase the rate of straw decomposition and eventual release of N compared to leaving straw on the surface (Schoenau and Campbell, 1996). In contrast, incorporation of legumes can release about 150 kg N ha^{-1} over 3 months (Berry et al., 2002). Cereal straw only contains about 35 kg N ha^{-1} compared with up to 150 kg N ha^{-1} for some vegetable residues. This has led some authors to suggest that including crops with a broad range of C:N ratios can help cycle and conserve N within the cropping system and can increase the soil capacity to supply N as needed for growing crops (Watson et al., 2002).

5.2. Nitrogen from animal sources

Animal manures are an important source of N in many integrated organic and low-input farming systems. Fresh manure has lower C:N ratios than composted manure, but is more difficult to store and transport if it is not from on-farm livestock. There is evidence that at least 50% of manure N is lost in storage and transport and another 25% is lost after application (Bouldin et al., 1984). Composted manures cause N to be held in more stable forms and are easier to store and transport, but because of the increased stability composting causes a significant decrease in short-term N availability. An incubation study by Tyson and Cabrera (1993) with composted poultry manure showed a gradual release of inorganic N, mineralizing 0.4–5.8% of the total N over 56 days compared with 25.4–39.8% of total N in uncomposted poultry manure. Despite lower N availability, composted manures have other benefits such as increasing soil pH to alleviate soil acidification from synthetic fertilizers that release inorganic N as ammonia (Tyson and Cabrera, 1993). Rather than being an immediate source of plant-available nutrients, composted manure has a longer-term role in building soil organic matter and stimulating microbial activity (Watson et al., 2002). One of the primary differences between organic and conventional N fertilizers is the release rate of inorganic N compounds. The capacity for plants to take up organic molecules containing N such as amino acids has been demonstrated, but is not yet well understood. Genotypic differences exist in wheat cultivars for the capacity to take up amino acids, and this may affect their performance in organic systems (Jennifer Reeve, unpublished data 2007). Despite this capacity, the majority of plant N uptake is likely to be inorganic N, so mineralization rates and timing of N availability from organic fertilizers is critical to understanding the NUE of cereals grown under organic management practices. Standard inorganic soil N tests are less useful for evaluating N availability in farming systems that rely on N derived from organic amendments (Watson et al., 2002). Organic systems usually do not have high levels of mineral N in the soil profile (Power and Doran, 1984), but often have greater mineralization potential due to higher levels of soil organic matter (Drinkwater et al., 1998; Stockdale et al., 2002).

5.3. Tillage regime

Soil disturbance and incorporation of surface residues and plant biomass have a major affect on N availability. Soil disturbance from mechanical tillage stimulates soil microbial activity which increases soil MIT and N availability (Watson et al., 2002). Increasing soil moisture after a prolonged dry spell, or thawing after freezing conditions also results in a flush of N mineralization (Cassman et al., 2002). When green manure crops are used as a source of N, incorporation is often used to accelerate the mineralization of organic N. Reliance on tillage, however, results in higher erosion risk. Reduced tillage or no-till management can minimize soil erosion, but can have both positive and negative impacts on N availability. For example, crop residues help prevent runoff, which reduces N losses, but surface residues can also immobilize N decreasing its availablity to the crop. Eliminating tillage often results in decreased nitrate concentrations in the soil profile compared to conventional tillage. Soon and Clayton (2003) reported residual nitrate levels two times greater in conventional tillage than no-till for the top 120 cm of soil. Increased N immobilization, leaching and denitrification in no-till systems can contribute to this phenomena (Schoenau and Campbell, 1996).

Although tillage affects N mineralization and availability, Soon and Clayton (2002) found that tillage regime did not have a significant effect on total crop N content. Similarly, in a study in the Palouse region of Washington, total aboveground N at maturity was the same for both conventional and no-till wheat, despite lower available N in no-till (Huggins, 1991). Reduced mineralization rates in no-till could limit grain yield if there were significant N deficiencies. This may be more critical in organic and low-input systems that depend on organic fertilizers and crop residues for crop nutritional requirements. In a study of barley and pea intercropping, the only treatment with net mineralization was incorporated pea residues. Mixed barley and pea residues and barley residues alone resulted in N immobilization, regardless of tillage, and pea residues alone without incorporation resulted in net immobilization (Haug-gaard-Nielsen et al., 2003). Dou et al. (1994) compared corn yields following a winter green manure killed using herbicides or tillage. Corn grown with conventional tillage did not suffer from N deficiencies, however, in the no-till herbicide-killed treatment there was significantly less N accumulation and corn yields responded to N fertilization. In addition, no-till corn had severe weed competition during the growing season which the authors attributed to lack of tillage for control. The N mineralization rates were very different for the two systems. In the conventional tillage system, there was rapid increase in mineralization rates during the first month, followed by a slower increase for the rest of the growing season. In the no-till system, there was a more gradual increase in mineralization rates during the first two months and then a leveling off of the mineralization rate. The study did not examine mineralization

the following year or the total net mineralization in the two systems.

A mixed tillage organic system provided comparable yields to a conventional, tilled system in a study done in Pennsylvania (Drinkwater et al., 2000). Study comparisons included a series of tillage treatments in conventional and organic systems. No-till organic methods produced very poor yields, partially because the green manure vetch did not germinate well in high residue conditions and only provided 75% of the amount of N provided by the vetch green manure in mixed-tillage system. Primary tillage caused a large amount of N mineralization, even though the total N produced was equivalent to the no-till mowed vetch. Management of the green manure with a chisel and disc was the only treatment that provided acceptable yields for the organic system while keeping soil mineral N pools at lower levels to prevent N losses. Cultivation for weed control in the organic systems also increased control of the timing of N mineralization. In an organic system, tillage and mid-season mechanical weed control may provide a needed N boost to growing crops, but could cause N leaching or denitrification if not taken up by the crop (Watson et al., 2002). The challenge is to time tillage so that it stimulates mineralization when the growing crop needs N, but so that it does not result in N losses from the system or excessive erosion. The effects of tillage on N cycling must also be balanced with the need for mechanical weed and disease control at certain points of the growing season, which may or may not correspond to the optimal time to stimulate N mineralization. This is an area that needs much more research if reduced tillage organic systems are to succeed.

6. Strategies for improving NUE

Cereal grain yields are often lower in organic than conventional systems, and problems with synchronizing crop demand for N with N mineralization explains part of this yield gap (Watson et al., 2002). Another portion of the yield gap may be because the cultivars that are compared in conventional and organic systems have been bred for conventional systems and thus are not adapted to organic conditions. Interestingly, the yield reduction sometimes observed when crops are grown organically is greater for crops that have had extensive modern breeding, such as wheat and barley, than for crops that have had relatively little breeding, such as oats or triticale (Watson et al., 2002). Even when varieties are tested under conditions of no added fertilizer N, this does not accurately represent soil and fertility conditions on organic farms, therefore, varieties selected with modern conventional breeding methods are unlikely to have optimal traits for organically managed systems. One particular difference between organic agriculture now and that before 1950 is that high-yielding crops such as hybrid corn have been developed which have a strong demand for N over a short time period, and this may not be easily compatible with organic fertilizers. This may be partly overcome by growing crops that have lower levels of N uptake and no sharp peaks in demand, such as wheat (Pang and Letey, 2000). It is also critical to breed crops that have the same high yield potential and are adapted to organic fertilizers and management practices. Adaptation to organic systems will require a suite of traits including nutrient use efficiency, durable disease resistance, competitive and allelopathic characteristics for weed suppression and quality and nutritional characteristics. This paper focuses specifically on the improvement of NUE, while recognizing the potential interactions among desirable traits in low-input and organic systems. Other traits are discussed in, for example, Ceccarelli (1996), Lammerts van Bureren et al. (2002), Mason and Spaner (2006) and Murphy et al. (2007).

6.1. Maintaining photosynthesis under N stress

Increasing the ability of leaves to continue photosynthesis under N stress is a potential avenue for improving NUE in agriculture. Increasing leaf production can increase the N recovery of perennial grasses, especially in the second year (Zemenchik and Albrecht, 2002). Perennials subjected to nutrient stress may rely more on N remobilization for leaf production. In an experiment with perennial grasses, new leaves contained 52% translocated N under low N conditions, compared to only 12% translocated N in plants growing under high N conditions, although the total amount of N translocated in the two treatments was similar (Li et al., 1992). In annual grains, the size and duration of active leaf tissue affects N uptake and the amount of plant N available for remobilization. Plants that do not senesce their leaves until very late have a greater capacity to take up N during grain fill because continued leaf activity promotes the uptake of soil N (Woodruff, 1972). Stay-green plants delay leaf senescence during grain filling, and may still have active leaf tissue when the grain is completely mature.

There may be a trade-off, however, between the efficient use of N for photosynthesis and leaf longevity. In short lived leaves, most N is allocated to photosynthetic structures and enzymes, while in longer-lived leaves it is necessary for the plant to invest in defensive compounds (Hikosaka, 2004). This trade-off may be more apparent when comparing different species rather than varieties within a species. In winter wheat, additional plant available N delayed leaf senescence and increased the amount of vegetative N which could then be translocated to the grain (Spiertz and Ellen, 1978). In some stay-green genotypes of maize, longer maintenance of leaf chlorophyll resulted in a 10–12% increase in grain weight (Spano et al., 2003). A study by Duncan et al. (1981) found that stay-green lines of sorghum had a greater leaf area duration and greater chlorophyll content than senescent types. Therefore, they may have greater photosynthetic capability which led to greater potential biomass and grain yield. Stay-green lines also established their adventitious root system earlier and always had greater root density than senescent lines. Also in sorghum, almost 70% of the total variation in grain yield was explained by total plant N content, and greater leaf N content may have allowed stay-green varieties to continue photosynthesis and N uptake under drought stress while senescent varieties had to rely on N and photosynthate translocated from the leaves and other tissues (Borrell and Hammer, 2000).

The interactions between N availability, late-season uptake, and remobilization are complex. Roots need a supply of photosynthate to absorb soil N, so late season photosynthesis helps maintain N uptake after anthesis (Kihlman-Falk, 1961). However, soil N deficiencies can also lead to early senescence because developing grain requires N that the plant supplies through remobilization of vegetative N (Lafitte and Edmeades, 1994; Sattlemacher et al., 1994; Spiertz and Ellen, 1978). Since remobilization of assimilated N requires degradation of leaf proteins and amino acids, it corresponds with leaf senescence and a decrease in photosynthetic activity. If soil N is limited or leaves are not producing enough photosynthate for both roots and developing grain, the plant is likely to slow or stop uptake after anthesis, which would make the N already present in the plant the only source of grain N at harvest. If more N remains in the leaves to maintain photosynthetic capacity, however, it is not available for remobilization to the grain, which could reduce grain protein concentration unless the plant can take up more soil N (Spano et al., 2003). Plants with rapid early-season N uptake, efficient remobilization and complete leaf senescence are likely to perform better in environments with severe N stress late in the season, but plants that are capable of late season uptake could have an advantage if environmental conditions make soil N available. Factors that contribute to late season uptake, such as increased root mass and depth, prolonged photosynthesis and greater leaf area can also help plants continue to fill grain when faced with drought stress.

6.2. Improved N uptake ability at low soil concentrations

Some species and varieties of plants have overcome limited nutrient availability through symbiosis with arbuscular mycorrhizal (AM) fungi. Although this has received much attention for its role in phosphorus acquisition, the symbiosis may also be important in N uptake, either through direct N transfer or enhanced plant nutritional status leading to increased uptake capacity (Azcón et al., 2001). Mycorrhizal symbiosis contributed to enhanced nutrient use efficiency in an experiment with lettuce, especially at low N concentrations in the growth medium. At high concentrations, the proportion of N derived from fertilizer decreased, particularly in those plants with AM fungal colonization (Azcón et al., 2001). This implies that mycorrhizal colonization may be beneficial for those plants when fertilizer N is not readily available, but that the symbiosis does not necessarily aid in fertilizer N uptake. Plants with complementary root architecture explore and utilize different parts of the soil profile and may transfer nutrients through AM fungi (Lynch, 2004).

Unfortunately, the ability to form mycorrhizal symbiosis may have declined in wheat cultivars bred after the 1950s as a result of higher levels of soil fertility in breeding programs making such symbiosis unnecessary and even detrimental to plant growth. Hetrick et al. (1993) found that in wheat's wild ancestors, the roots of all accessions tested were colonized by mycorrhizal symbionts but not all the accessions showed a positive growth response. For landraces, or traditional farmer varieties, mycorrhizal colonization did increase plant growth, with the strongest response observed in landrace accessions from Asia (China, Turkey, Afghanistan and Korea), leading the authors to speculate that perhaps the cultivation of wheat in monoculture without fertilization indirectly selected for increased mycorrhizal dependence (Hetrick et al., 1992). If landraces were selected for increased productivity compared to their wild ancestors, this could have increased both the demand for soil nutrients and plant nutrient losses because of the relationship between growth rate and nutrient turnover. Higher levels of root exudates could have favored the development of mycorrhizal symbiosis in early agricultural systems.

In more modern cultivars, the benefits plants received from colonization ranged from positive to neutral to negative. The fact that cultivars show variable responses to colonization suggests that there may be two sets of genes involved, one for the process of colonization and the other for nutrient acquisition by the plant (Hetrick et al., 1993). Winter wheat cultivars appeared to form beneficial symbiosis up until 1950, but cultivars released after that time have inconsistent relationships with mycorrhizae, including reduced growth after colonization. This may be a result of modern breeding in highly fertile soils, and it remains to be seen whether breeding programs deliberately conducting selection in low-input environments will select for increased colonization and symbiosis.

The effects of plant root exudates on the rhizosphere environment is of interest to low-input and organic systems because of the potential to increase the availability of nutrients to the plant. Microbial biomass can strongly influence the dynamics of mineral N in the soil (Nieder et al., 1996). A full review of the soil–plant–microbial interactions affecting nutrient availability is beyond the scope of this paper, however, there is evidence that plant species and genotypes within species may have differential effects on rhizosphere microorganizms and nutrient availability (Cheng et al., 2003; Rengel and Marschner, 2005). With perennial crops, the ability of the plant to modify the rhizosphere environment may be even more critical. As plants release N-containing compounds through root sloughing when above-ground material senesces in autumn, having strong symbioses with mycorrhizae or beneficial root-zone microorganisms may enable the plant to recapture this N during spring regrowth, increasing the functional N_c. In a study of a native grass species, *Poa pratensis* L., which had coevolved with grazing animals, Hamilton and Frank (2001) found that defoliation of plants led to increased carbon exudates, which stimulated rhisospheric microbial population growth. This, in turn, led to higher levels of available N, which increased N uptake, shoot N and rates of photosynthesis in the recovering plants. Selection of plants with high levels of crown and tissue N plus useable rhizosphere N and vigorous spring growth may increase the performance of perennial grains more than selection only for grain yield and protein characteristics or for fast vegetative growth in autumn.

In addition to selecting for the ability to form symbioses, it is important to increase root affinity for soil N at low N concentrations. A study of wheat cultivars released over the

past several decades shows that historic cultivars have better ability to extract and use soil N when there was no added fertilizer (Foulkes et al., 1998). In contrast, more recent cultivars were more responsive to high N supplies. It is likely that improvements in fertilizer use in modern varieties are due to increased rates of N uptake during the period following N fertilizer application. The decrease in soil N uptake capacity may be because of less vigorous early growth and rooting in semi-dwarf cultivars (Foulkes et al., 1998). A comparison of tall and semi-dwarf varieties showed that yields were similar under high-N conditions, but that tall genotypes performed better in low-N treatments (Morris and Paulsen, 1985). These changes over time indicate that modern breeding may have created varieties that are not well-suited to low-input or organic systems. These systems are much more complex than experimental systems where N is limiting and all other management factors are optimal. Because low-input and organic systems rely much more on biological cycling of nutrients, NUE in these systems will be closely linked to management and genetics that synchronize crop demands with N availability.

7. Conclusion

Low-input and organic agricultural systems present unique environmental conditions and objectives not present in either conventional agriculture or natural ecosystems. The ideal crop plant would be adapted to low N conditions while still producing high yields of nutritious grain for human consumption. The evolutionary trade-off between high productivity and adaptation to low nutrient environments presents a challenge to this goal. However, plant breeders often select for increases in negatively correlated traits, and with careful selection strategies, it may be possible to improve NUE in both an agricultural and ecological context.

Breeding for high input systems may have increased the relative N requirement of crop plants, while natural selection on crop wild relatives has perhaps increased the mean residence time at the expense of N productivity. Because breeders are able to utilize germplasm from both elite cultivars and wild species, the beneficial traits from both of these gene pools may be combined and selected specifically for performance in sustainable agricultural systems. More research is needed to better understand the N dynamics of low-input and organic systems and to develop effective selection tools. Methods of selecting both annual and perennial crops for symbiosis with soil microorganisms need to be developed. A better understanding of the partitioning of N in perennial species and the proportion of total N uptake that is carried over to the subsequent season is also needed.

Most likely, there is an optimal balance of N conservation and N productivity that falls somewhere between that of natural ecosystems and that of conventional agriculture. This optimum will depend on management practices and climactic conditions. To achieve both agricultural and ecological goals, it is necessary to develop crop varieties using a combination of agricultural and ecological NUE concepts.

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