Dual Role of Nitrogen: Essential Plant Mineral Element and Source of Inorganic Pollution

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Abstract

Increased demand for food products in modern agriculture is attributed to the application of chemical fertilizers which generally possess damaging environmental impact. Nitrogen is an essential mineral element required in large amounts for normal growth and development of plants, and nitrogen-based fertilizers are of particular importance since they may increase nitrogen use efficiency and consequently can lead to better plant yield and productivity. The regulation of nitrogen metabolism in plants is very complex and conditioned with both physiological processes in plants, as well as environmental factors. Although the use of nitrogen fertilizers resulting in significant increases in crop yield, the applied fertilizers are used by plants in small amounts, whereas more than 50% is lost by leaching, runoff, or microbial activity. In this chapter, we discuss main plant mechanisms regarding nitrogen absorption, translocation, and assimilation

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M. Hasanuzzaman (ed.), *Approaches to the Remediation of Inorganic Pollutants*,
https://doi.org/10.1007/978-981-15-6221-1_3

together with environmental factors affecting nitrogen metabolism with a special focus on the possibilities to overcome problems caused by nitrogen fertilizer usage.

Keywords

Absorption · Assimilation · Fertilization · Mineral nutrition · Nitrogen

Abbreviations

AMT	Ammonium transporters
GOGAT	Glutamate synthase
GS	Glutamine synthetase
HATS	High affinity transport system
LATS	Low affinity transport system
N	Nitrogen
NH_4^+	Ammonium ion
NiR	Nitrite reductase
NO_3^-	Nitrate ion
NR	Nitrate reductase
NRT	Nitrate transporters
NUE	Nitrogen use efficiency
NUpE	Nitrogen uptake efficiency
NUtE	Nitrogen utilization efficiency

1 Introduction

For the main processes of plant growth, development, and reproduction, availability of nutrients together with the absorption and conversion of solar energy are mandatory (Attaran et al. 2014; Jakovljević et al. 2017). The fundamental processes during which plants assimilate carbon and nitrogen into components necessary for growth and development are conditioned by the selective partition of primary and secondary metabolites between organelles, cells, tissues, and organs. The diversity of the produced metabolites is wide, as well as the pathways through which metabolites are incorporated, and the synthesis and incorporation are also partitioned between plant main structures (Tegeder and Weber 2006; de Wit et al. 2018).

Roughly, plant nutrient requirement can be assessed through the inorganic composition of the plants, since plant dry matter constitutes 10–20% of the fresh weight, while nearly 10% of the dry matter consists of mineral elements (Reddy and Raghavendra 2006). The low level of availability of a particular element in the soil or its increased concentration most often leads to nutritional stress. Continuous deficiency/excess of essential elements is usually accompanied by visual symptoms and morphological changes on the plant itself, which include changes in color, loss of chlorophyll, necrosis, etc. As sessile organisms, plants are very often limited with the unfavorable concentrations of an essential element in soil, and to survive in a nutritionally unfavorable environment, they need to adapt at the biochemical and physiological level and adjust development according to the available elements. Nitrogen (N), phosphorus (P), and potassium (K) are mandatory for plants for normal growth and development, however, soil supply of these elements is often limited in different areas of plant cultivation. To achieve better crop yield farmers usually increase the amount of fertilizers leading to damage to soil structure and nutrient status. In addition, the damaging environmental impact of nitrogen N-fertilizers on global nitrogen cycle is noticed (Robertson and Vitousek 2009; Araus et al. 2020).

Taking into consideration the amount of fertilizers applied in agricultural ecosystems together with pollution caused by increasing nitrogen-based fertilization, this chapter provides information about ecophysiological bases of absorption and assimilation of different forms of nitrogen, plant adaptations to the variations of nitrogen concentration, as well as potential solutions to overcome the problems caused by excessive intake of nitrogen-based pollutions.

2 Nitrogen as an Essential Mineral Element

The nitrogen (N) is, in the largest amount, stored in the atmosphere in the unreactive N_2 (gaseous) form (Stevens et al. 2011). In general, on continents and in the oceans, biological N_2 fixation (biological reduction of atmospheric N_2 to ammonium) is the starting point of biological N turnover. Although it is significantly higher on land than in oceans, the denitrification is almost identical on land and in the ocean. Additionally, the N cycle is particularly affected by industrial N_2 assimilation resulting in NH_3 production. The N fixation provides about 65% of the biosphere's available nitrogen (Lambers et al. 2008; Mokhele et al. 2012).

As a constituent of amino acids and nucleic acids, nitrogen is an essential component of plant cells at the structural, genetic, and metabolic levels and is involved in many processes of growth and development. Due to its key role in chlorophyll production, nitrogen is fundamental for the photosynthetic process; as part of various enzymatic proteins nitrogen regulates growth processes; contributes to the protection against parasites and diseases; and affects crop yield and biomass (Muñoz-Huerta et al. 2013).

2.1 Nitrogen Absorption

While the inorganic forms of nitrogen are produced by soil microorganisms and represent less than 5% of total nitrogen, nitrogen is present in organic forms at levels lower than 1% of the total soil volume (Araus et al. 2020). The content of organic and inorganic nitrogen sources in the soil is heterogeneous and dynamic, and depends on a different soil factors, such as temperature, pH, chemical properties, and the presence of microorganisms (López-Arredondo et al. 2013). Inorganic nitrogen is available in soil in two forms, as the NO_3^- (nitrate) ion and as the NH_4^+ (ammonium) ion and is absorbed by the roots. It is known that the soil water regimes affect the availability of nitrogen forms and nitrogen and water status have both synergistic and antagonistic effects of root architecture and stomata aperture (Araus et al. 2020). Besides the fact that the nitrate ions can very easily be found mainly in deeper layers of the soil, and that much more energy is required for these ions to be reduced compared to ammonia absorption, for most of the dry environment or agricultural soil plants, nitrate ions are major nitrogen sources. In contrast, ammonium ions are favorable in humid environments and forest habitats (Harrison et al. 2007; Christophe et al. 2011). In addition, since the concentration of nitrate ions in the soil varies over a wide range (from 10 μM to 100 μM), non-leguminous plants must adapt to the spatial and temporal fluctuations in the availability of this essential element (Miller et al. 2007; Christophe et al. 2011).

The regulation of nitrogen metabolism in plants is very complex and influenced by both physiological as well as metabolic processes such as nitrogen metabolite level, circadian rhythms, and sucrose synthesis and transport. Additionally, different plant species respond to nitrogen availability through the modification of root architecture, remobilization of nitrogen storage, and activity of the transport system (López-Arredondo et al. 2013). It is known that when it comes to nitrogen absorption plant roots possess multiple transport system, and one active and one passive transporter for ammonium absorption. These transport systems require mechanisms for root to shoot signaling as well as signal transduction within the root (Glass et al. 1999).

During the vegetative phase, meristematic tissue and developing organs require large amounts of nitrogen to synthesize and store amino acids that are incorporated into proteins. However, excessive quantities of ammonium have detrimental effects on plant growth and may lead to ammonium toxicity (Domínguez-Valdivia et al. 2008; Hachiya and Sakakibara 2017; Jakovljević et al. 2017). At the molecular level, the adaptation to variation in the amount of available nitrogen is based on the presence of nitrate and ammonium transporters whose affinities vary. According to Hachiya and Sakakibara (2017), the root nitrogen net influx consists of total nitrogen influx and total nitrogen efflux, and specific transporters of nitrate (NRT) and ammonium (AMT) contribute to the total nitrogen influx, except for high ammonium nutrition. Regarding the high affinity ammonium transporters (AMT1) the different plant species show regulation of the expression at the transcriptional level; the transporters are mainly induced in roots of plants deprived of nitrogen and downregulated after ammonium re-supply (Rogato et al. 2010). When the soil nitrogen concentration is below 1 mM, the high affinity transport system (HATS) is predominant, while the low affinity transport system (LATS) is predominant for nitrogen concentrations above 1 mM (Fig. 1). The main component of HATS is the plasma membrane proteins of the epidermis, cortex, and endodermis of the root, and their synthesis is regulated by the NRT2 gene family. Part of the LATS are proteins (controlled by the NRT1 gene family involved in the regulation of root development and auxin transport) that are located in the root epidermis, cortex, and endoderm. (Little et al. 2005; Hermans et al. 2006; Remans et al. 2006; Christophe et al. 2011;

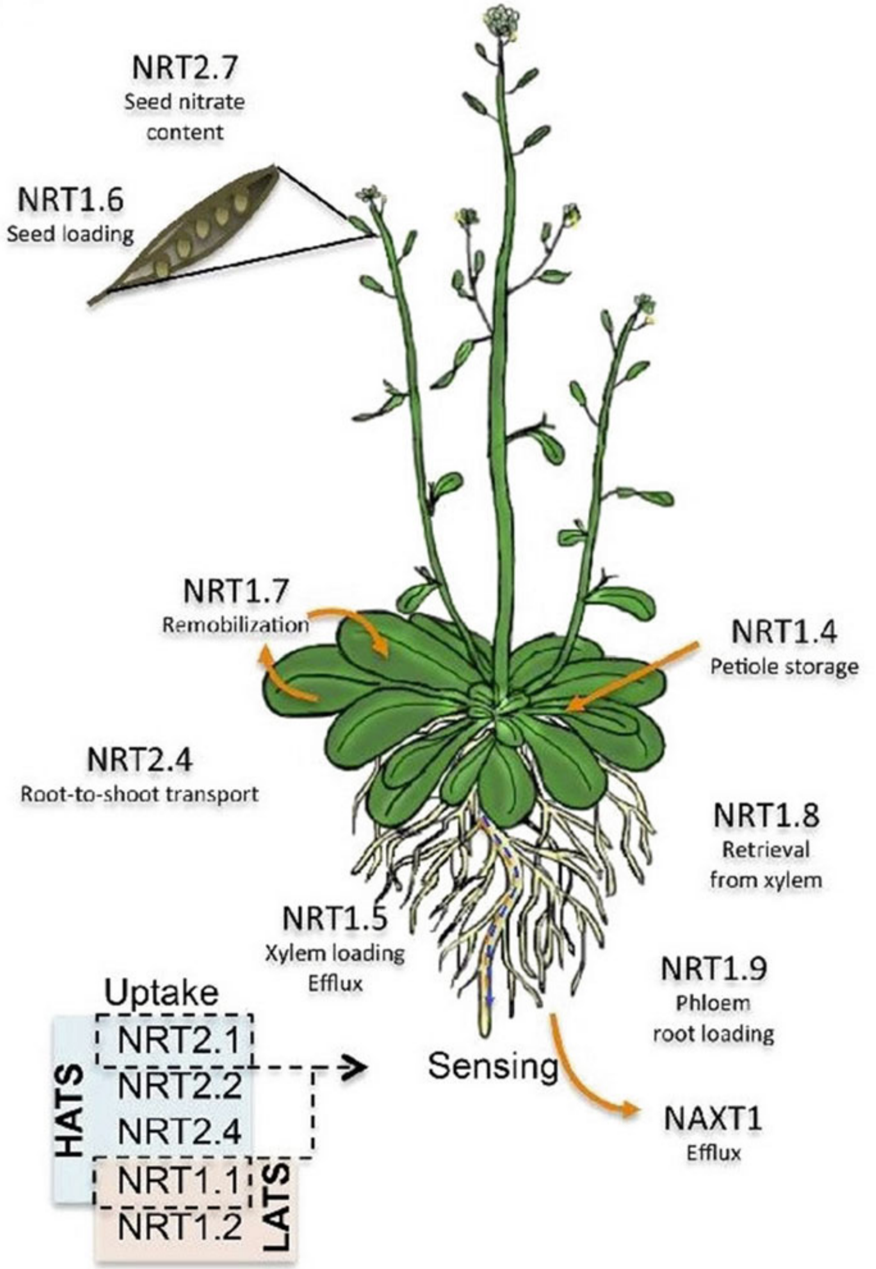

Fig. 1 Transporters and regulatory elements involved in nitrate metabolism according to López-Arredondo et al. (2013); by numerous transporters nitrate is absorbed through the root system and allocated to the different tissue

Bai et al. 2013). For a detailed explanation of the complex network of proteins included in nitrogen uptake, transport, and assimilation in plants see López-Arredondo et al. (2013); for the possible existence of a plant root derived mechanism for sensing the ammonium external concentration and achieving a convenient modulation of the root development in conditions of potentially toxic external ammonium concentration see Rogato et al. (2010).

2.2 Nitrogen Assimilation

For plant growth and development nitrogen assimilation into carbon skeletons represents a physiological process of the utmost importance. Inorganic nitrogen is assimilated into glutamate, glutamine, and asparagine—amino acids with an essential role as nitrogen-transport compounds in plants (Lea and Miflin 2003; Mokhele et al. 2012).

The nitrate assimilation takes place mainly in the plant roots, and it is dependent on the age and limitation of space for root growth (Marquez et al. 2007). According to Aslam et al. (2001) plants that exhibit low rates of nitrates in roots export absorbed nitrates to the shoots where it is reduced and incorporated into amino acids. Since the ammonium is the only reduced nitrogen form available to plants for assimilation into amino acids (Ruiz et al. 2007), absorbed nitrate needs to be further reduced to ammonium.

Once it enters the cell, the nitrate ion is subject to reduction. Nitrate reduction is always carried out in two steps—first to nitrite and then to ammonium ions by nitrate reductase (NR) and nitrite reductase (NiR). Since the reduction of nitrate to ammonium via NR and NiR requires eight moles of electrons per mole of nitrate, the ammonium utilization significantly decreases the energy consumption for organic nitrogen compound synthesis (Hachiya and Sakakibara 2017). The reduction of nitrate is dependent on the plant species, the amount of nitrate available, and the energy required. It is also tissue specific. Assimilated nitrates can be reduced in the root or in the aboveground organs, and further reduction and synthesis of organic compounds are done in leaves (Schjoerring et al. 2002). NR uses NADH as an electron donor in the nitrate reduction process, and this process takes place in the cytoplasm. The resulting nitrites are further reduced by NiR in chloroplasts of leaf cells or in root cells. Due to the highly reactive nature of nitrites, plant cells immediately transport them from the cytosol into chloroplasts in leaves and plastids in roots, and in these organelles, nitrites are further reduced to NH_4^+ via NiR. In leaves the electrons for reduction are derived from the reduced ferredoxin from the photosynthetic electron transport chain (ETC), while the root and leaf cells in the dark are supplied by electrons from respiratory metabolism (NADH) (Stitt 1999; Rosales et al. 2011).

Due to their high toxicity even at low concentrations, as well as the possible disruption of the respiratory process, ammonium ions must be assimilated into non-toxic organic components in the shortest amount of time. Toxic effects of ammonium are the consequence of proton extrusion, changes in cytosolic pH, as well as uncoupling of photophosphorylation in plants (Wang et al. 2007). The assimilation of ammonium takes place in root cells. NH_4^+ ions, formed either by nitrite reduction or by direct assimilation of ammonium, are immediately assimilated by the glutamine synthetase-glutamate synthase (GS/GOGAT) cycle. This system provides entry for reduced inorganic nitrogen into all plant nitrogen-containing organic compounds. GS catalyzes the ligation of ammonia and glutamate to glutamine, while GOGAT catalyzes the redox transfer of the glutamine amide group to α-ketoglutarate, forming two glutamate molecules (Dragićević et al. 2016). The pivotal role in ammonium assimilation have the GS which activity is critical and rate-limiting (Mokhele et al. 2012). The enzyme activity of the GS-GOGAT system is regulated by genes responsible for the synthesis of plastid and cytoplasmic glutamine synthetases and GOGAT. Assimilation is accompanied by the synthesis of organic acids, primarily α-ketoglutaric acid (which serves as an ammonium acceptor in the GOGAT system) and malate, which prevents alkalization. In addition, transcription of NIA and NII genes encoding proteins involved in the synthesis of these amino acids is significantly increased, as is the activity of the corresponding enzymes (Raab and Terry 1995; Stitt 1999; Schjoerring et al. 2002).

Glutamic acid (which always exists in plant cells in a certain amount) receives NH_4^+ ion and is converted to glutamine by ATP and GS enzymes. GOGAT then catalyzes the transition of the amino group from glutamine to α-ketoglutaric acid, producing two glutamic acid molecules. The glutamic acid formed is partially recovered and partly used to build nitrogen-containing compounds. These two reactions that are generally referred to as the GS/GOGAT cycle are nowadays accepted as the primary route of nitrogen assimilation in plants. Cytosolic GS1 and plastidic GS2 are two GS isoenzymes with different locations in subcellular compartments (Mokhele et al. 2012). In higher plants, GOGAT is represented in two different isoforms—NADH-dependent GOGAT (NADH-GOGAT) and ferredoxin-dependent GOGAT (Fd-GOGAT). NADH-GOGAT is, above all, active in non-photosynthetic tissue and young growing organs. The expression of genes responsible for the synthesis of Fd-GOGAT (GLU1 and GLU2) is tissue specific. GLU1 genes are dominant in leaves, whereas GLU2 genes are expressed in the root (Lam et al. 1996; Oliveira et al. 1997; Temple et al. 1998; Stitt 1999). The pathway of nitrogen metabolism and incorporation into organic compounds is presented in Fig. 2.

3 Environmental Factors Affecting Nitrogen Absorption and Assimilation

Despite the fact that certain critical level of nutrients is obligatory for plant normal growth and development, the mineral composition of plants shows wide variations and is under the influence of the plant age, the genetic constitution of the plant, chemical constituents of the soil, as well as climate conditions (Reddy and Raghavendra 2006). Under the conditions of natural field plants faced changing environments where nitrogen concentrations vary and may be limiting for growth

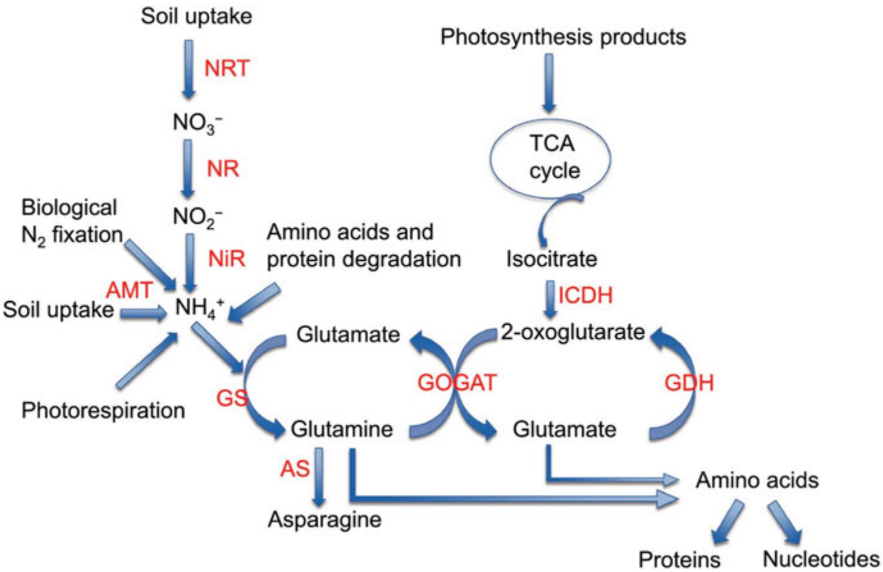

Fig. 2 Pathway of nitrogen assimilation and incorporation of nitrate or ammonia into amino acids and other molecules in higher plants according to Lu et al. (2016). NRT nitrate transporters, NR nitrate reductase, NiR nitrite reductase, AMT ammonium transporters, GS glutamine synthetase, GOGAT glutamate synthetase, AS asparagine synthetase, GDH glutamate dehydrogenase, ICDH isocitrate dehydrogenase

together with C/N ratio in the soil and within the plant, as well as rainfall, temperature, and soil type. Therefore, it is required for plants to maintain the optimum nitrogen and carbon for normal root and shoot development, photosynthetic rate, synthesis of amino acids, organic acids, and lipids (Kant et al. 2011). In general, nutrient stress is a complex phenomenon since may originate from either low levels or by the presence of excess concentrations of the element, whereas, in some cases, the presence of one element in excess concentrations may induce the deficiency of another element (Reddy and Raghavendra 2006). Inappropriate amount of nutrients directly affects photosynthetic apparatus through the functioning of major photosynthetic components (Kalaji et al. 2014; Jakovljević et al. 2017). According to Clay et al. (2006), nitrogen stress reduces chlorophyll production, and reduced chlorophyll content may lead to increased reflectance of photosynthetically active light and nitrogen-stressed plants appearing yellow. In addition, the photosynthetic apparatus is the main endogenous source of reactive oxygen species even during coordinated physiological processes and inappropriate functioning may result in cell death (Foyer and Shigeoka 2011). Therefore, adaptation to the conditions of limiting mineral nutrition is an important survival strategy (Kant et al. 2011).

Generally, a low level of nitrogen in the soil leads to the reduction of photosynthesis, root growth inhibition, suppression of plant lateral root initiation as well as leaf senescence. The high environmental concentration of nitrate inhibits lateral root elongation mainly due to the accumulation of this ion together with nitrogen metabolites inside the plants (Kant et al. 2011). Morphologically, nitrogen deficiency is accompanied by rapid plant growth inhibition. Due to the mobilization of nitrogen in older leaves, young leaves may not show symptoms of deficiency; however, within persistent deprivation older leaves become yellow and fall of the plant. Additionally, plants have woody stems since carbohydrates cannot be used in the synthesis of nitrogen-containing compounds (Briskin and Bloom 2010). It is known that ammonia excess has detrimental effects on plant physiology through the induction of stress and oxidative imbalance in plants (Jakovljević et al. 2017, 2019). Additionally, hazard effects of this ion can also be seen through the soil acidification and soil nutrient leaching, as well as water pollution.

The effects of different nitrogen forms are interesting for agriculture, particularly due to the potential of organic nitrogen to enhance nitrogen use efficiency (Franklin et al. 2017). Nitrogen use efficiency (NUE) can be defined as the yield of grain per unit of nitrogen (both natural and applied) available in the soil (López-Arredondo et al. 2013) and it may be concluded that increasing NUE of the crops is a possible strategy of reducing nitrogen fertilizer losses in agriculture. As is suggested by Garnett et al. (2009), plants can increase utilization efficiency (doing more with the less), or can increase uptake efficiency; plants developed with improvement in both cases will be the solution, however, improvement in either trait would be beneficial for the present. In any case, it is important to gain a better understanding of the function and regulation mechanism of the main components involved in N absorption, transport, assimilation, and signal transduction to improve the NUE in crops (Li et al. 2017).

The NUE with two components (nitrogen uptake efficiency (NUpE) and nitrogen utilization efficiency (NUtE)) depends on morpho-physiological characteristics of plant species, as well as complex interactions between plant and environment. The relationships between plant growth, nitrogen dynamics, and nitrogen use efficiency for rapeseed (*Brassica napus* L.) are illustrated on Fig. 3.

4 Nitrogen Fertilizers and Environmental Pollution

Due to the natural depletion or leaching, nitrogen must be added to the soil (Mokhele et al. 2012). According to Kant et al. (2011) increase in crop productivity is associated with a 20-fold increase in the global use of nitrogen fertilizer applications during the past decades and it is expected to increase several times by 2050. Additionally, the large amount of fertilizers used in developed countries helps prevent fluctuating levels of nitrogen, however, as a consequence, a lot of fertilizers is wasted to the environment.

The most commonly used nitrogen fertilizer in agriculture is urea, about half of all used fertilizers for crop production (Witte 2011; Mokhele et al. 2012). It is taken by plants actively from the soil, and after uptake into the plant cells, the assimilation is catalyzed with urease (urea amidohydrolase) and urea amidolase which hydrolyze urea in the cytosol to CO_2 and NH_3 (Wang et al. 2007). The addition of urea, as well

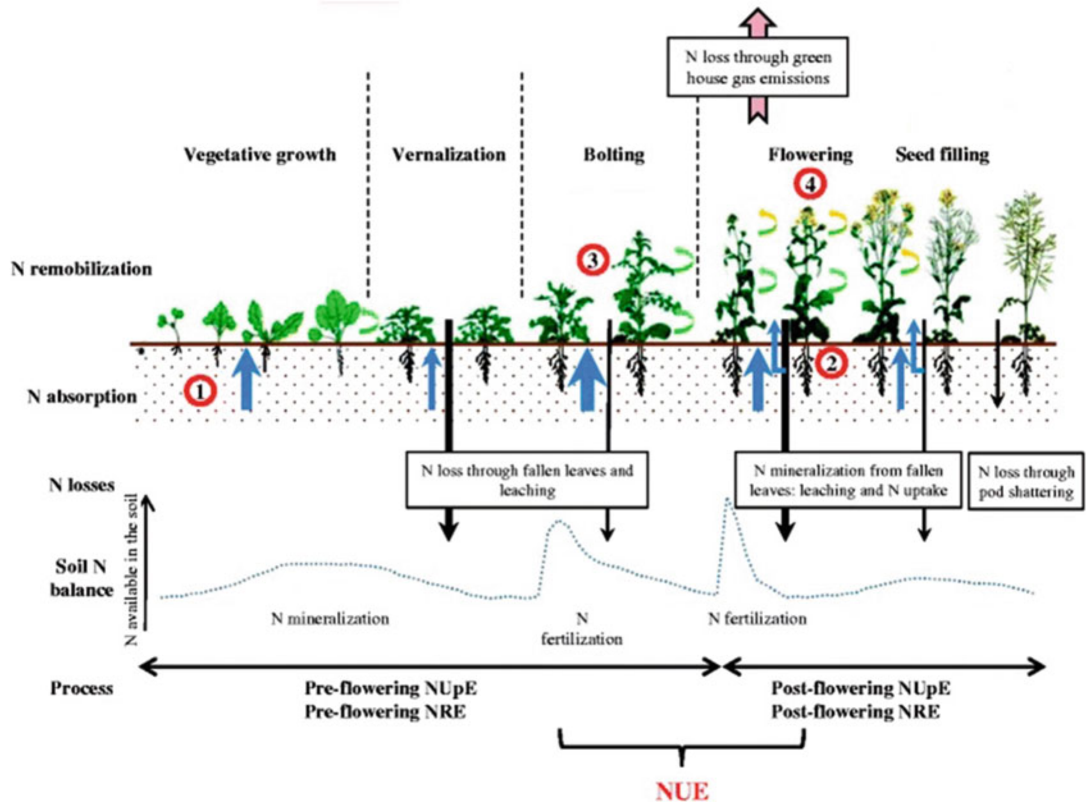

Fig. 3 Illustration of the relationship between *Brassica napus* L. growth, nitrogen dynamic, and yield over the crop cycle with the critical stages for the final establishment of NUE (according to Bouchet et al. 2016, with some modifications); blue arrows represent nitrogen uptake (width indicates the relative amount of absorbed nitrogen); black arrows represent nitrogen losses (width indicates the relative amount of nitrogen lost at a given point of time). NUE nitrogen use efficiency, NUpE nitrogen uptake efficiency, NRE nitrogen remobilization efficiency

as other nitrogen fertilizers, is the highest input cost for many crops. However, these compounds are highly mobile through the soil and crop plants can utilize only 30–40% of applied fertilizer leading to loss of more than 60% (Kant et al. 2011). The main processes of nitrogen fertilizer loss contributing to environmental pollution are combinations of nitrate leaching, soil denitrification, volatilization, and microbial consumption (Zebarth et al. 2009). The nitrate leaching contributes to eutrophication through the water contamination, while volatilized nitrogen contributes to global warming through the nitrous oxides releasing. Also, high nitrogen supply may become dangerous to human health through the high concentration of nitrogen forms in plant leaves (Muñoz-Huerta et al. 2013).

As mentioned, the reactive forms of nitrogen are utilized by organisms and naturally enter the ecosystem via biological N fixation, but human activities have more than doubled the input of nitrogen into the World's ecosystems over the last century (Stevens et al. 2011). According to Van Wijk et al. (2003), the response of ecosystems to increased nutrient ability is influenced by the plant characteristics and chemical and microbial immobilization. Stevens et al. (2011) noticed that although in Europe and parts of North America the deposition of NHx (ammonia and ammonium) and NOy (nitrate, nitric oxides and nitric acid) increased in the second half of twentieth century mainly due to industrial and agricultural activities, the significant differences are even seen at the continental scale. Figure 4 illustrates the main differences.

5 Concluding Remarks and Future Challenges

A marked increase in food production attributed to the application of chemical fertilizers results in climate change, environmental pollution, and biodiversity loss, which is an enormous environmental challenge of the twenty-first century since the application of nitrogen fertilizers will keep increasing with the growing demand for food (Godfray et al. 2010; Liu et al. 2013; Li et al. 2017). At the same time with nitrogen-based fertilizer underline of modern agriculture, the damaging environmental impacts including disruption of the global nitrogen cycle are already being left (Araus et al. 2020). Therefore, nitrogen fertilizer based pollution is a serious issue for many regions with highly concentrated agriculture, and in order to minimize the footprint of agricultural production there is a particular interest to develop technologies which allowing economical production with minimum applied nitrogen (Garnett et al. 2009).

One of the effective solutions may be the cultivation of plants tolerant to low nitrogen in order to reduce the amount of fertilizers, as well as to avoid excessive waste (Li et al. 2018; Jakovljević et al. 2019). The field management in general and reduction of nitrogen losses through improved field management are essential in order to optimize nitrogen losses. Some of the techniques involved are the better coordination of nitrogen/water status in the soil, the application of fertilizers in appropriate growing season and irrigation or rainfall time, as well as better matching of fertilizers with the particular crop and soil (Garnett et al. 2009; Araus et al. 2020).

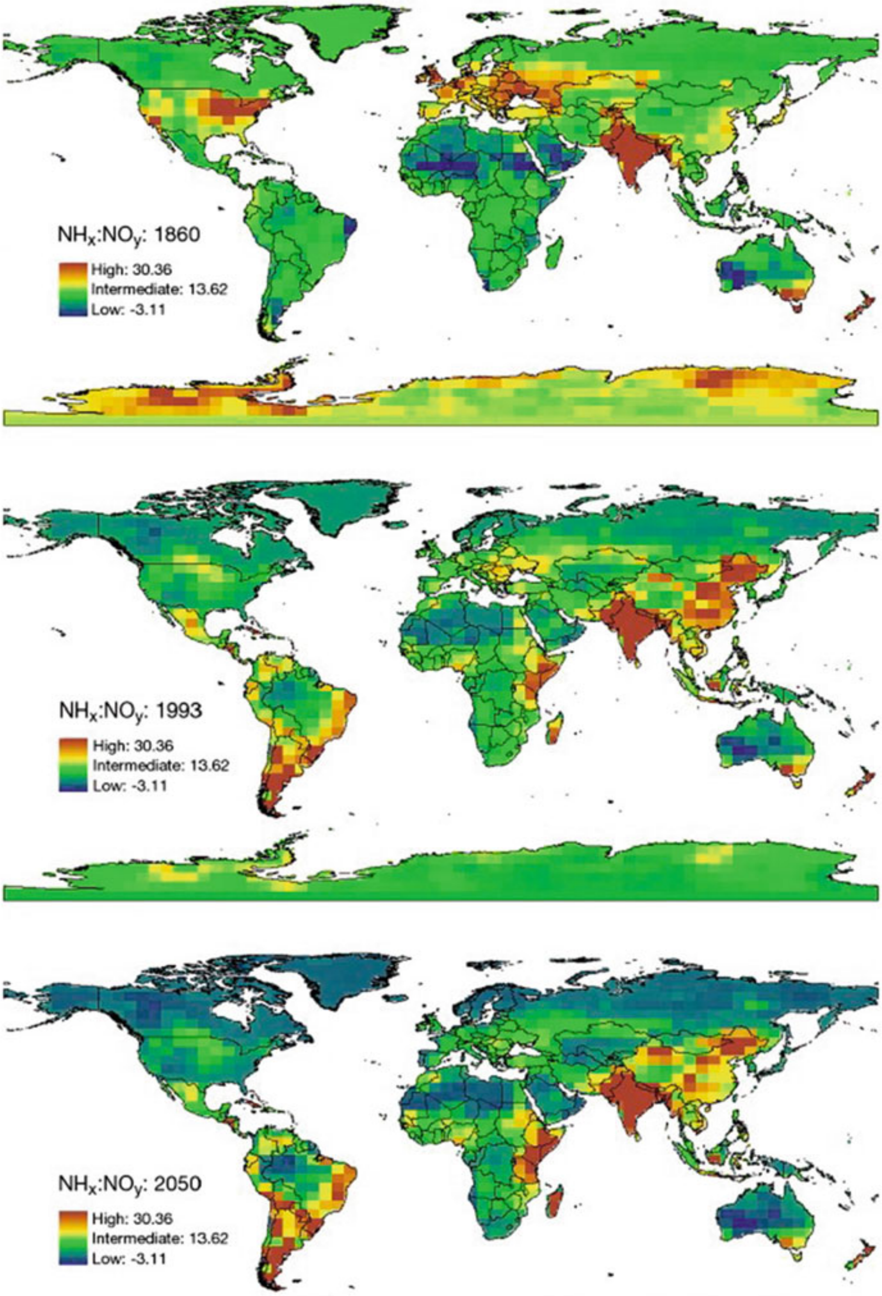

Fig. 4 Illustration of main differences in the NHx (ammonia and ammonium) and NOy (nitrate, nitric oxides, and nitric acid) inputs at the continental scale (accordin to Dentener 2006 and modified by Stevens et al. 2011)

Having in mind that with a 1% increase in NUE approximately US$1.1 billion could be saved, a promising way to deal with this crisis is an improvement in crops nitrogen use efficiency (Kant et al. 2011; Li et al. 2017). Potential targets of NUE improvement are nitrogen assimilatory enzymes and root morphology, since at the end of the growing season, particularly in rapidly leaching or in drying nitrogen depleted soils, root architecture may be of great importance (Garnett et al. 2009). Therefore, breeding plants with deeper root systems or with the ability to elongate roots into deeper soil layers may adapt plants to low nitrogen and low water conditions (Arai-Sanoh et al. 2014; Araus et al. 2020).

As is suggested by Díaz et al. (2019) many modern cultivars may be without genetic diversity opposite to their wild varieties, leading to an aggravated growth under low nitrogen environment. Consequently, researches focused on plant species with diverse phylogenetic origins and their adaptations will help to find a solution for plant survival in the dry and nutrient-poor environment (Araus et al. 2020). Continuous investigations are of great importance with a better understanding of soil environment, plant characteristics, and changes of these characteristics with the changing environment.

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