Chapter 1
Physiological Basis of Plant Nutrient Use Efficiency – Concepts, Opportunities and Challenges for Its Improvement

Martin Reich, Tahereh Aghajanzadeh, and Luit J. De Kok

Abstract Knowledge on the underlying physiological processes and variables which bias their contribution to nutrient use efficiency (NUE) is crucial to develop strategies for improvement in agroecosystems. This chapter aims to contribute to the understanding of the physiological basis of NUE to develop strategies for improvement by modern breeding, but also conceive the challenges and current limits to do so. General concepts will be summarized briefly and broken down to the main components before, in the main part of this chapter, the involved physiological processes are reviewed and discussed in their relation to NUE. This is followed by an identification of the factors that make the individual contributions of these processes to NUE so variable and impede one general concept for all crops, environmental conditions and nutrients. The last part of the chapter is dedicated to a critical analysis of the opportunities and challenges to improve NUE, which arise from physiological interactions and trade-offs on a whole plant level.

Keywords NUE (nitrogen use efficiency) • Nitrogen • Agroecosystem • MRT (mean residence time) • Crop yield • Oscillations • Acquisition efficiency • Utilization efficiency

Introduction

Plants are principally, as are all living organisms, chemical compartments, which are in thermodynamic disequilibrium with their environment. This is actively maintained by the utilization of solar energy for driving selective chemical exchange with the environment. In addition to carbon dioxide and water, which provide the structural and metabolic backbone elements C, O and H, the complex functioning of plants requires the uptake of at least 13 additional essential nutrients from the soil. Nutrients can be classified into two very distinct groups depending on

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their concentration in plant tissues (macro- and micronutrients), and the specific roles they fulfil in the plant's metabolism are as diverse as their physiochemical properties (Marschner 2012).

Plant NUE is a term, which describes a highly complex, multigenic trait with various interconnected physiological processes involved and modified by numerous factors. Consequently, there are numerous approaches to define, analyse and possibly improve NUE. For a long time it has been known that the ability of plants to utilize nutrients can differ substantially between species and cultivars, and that this could be the basis for further improvement through breeding (Gerloff 1963; Shea et al. 1968; Siddiqi and Glass 1981). In order to develop a common framework for NUE, scientists started to formulate concepts and definitions that should serve as a basis for comparison and discussion of research. Since then countless studies in various scientific disciplines dealing with different plant species, in different contexts, under different conditions and focusing on different nutrients failed to find one definition of NUE that describes all cases satisfactory but rather revealed that the issue is too complex to do so.

In this chapter the definition of NUE will be discussed from a whole plant perspective. It starts with the transfer of NUE from an ecological to an agronomical context and the different levels of organization on which it can be discussed. This is followed by a brief introduction into the conceptual framework of NUE, especially for nitrogen (N) and equipped with these theoretical concepts the attention of the reader will be drawn to the concrete physiological basis of NUE. These processes are the targets of potential improvement of NUE for agricultural production by modern breeding. However, how relevant a certain physiological process is in a particular cropping system depends on three main variables: environment, plant and nutrient, which influence the physiological basis of NUE. The last parts of this chapter are dedicated to the need to improve NUE in modern agriculture and ends with a critical review of the chances and challenges to improve plant NUE from a whole plant perspective.

Nutrient Use Efficiency – Contexts and Concepts

A general definition of "efficiency" is: *The achievement of an intended outcome with a lowest possible input of costs*. While the input in the concept of NUE obviously is nutrients, the *intended outcome* needs to be further specified. This can happen in different ways, which leads to many different versions of what NUE actually means and how it can be improved. Very fundamental is the difference between an ecological and agronomical context. Understanding this difference is crucial to develop strategies of improving a plant with its complex ecophysiological background in the straightforward input-output system of agriculture.

The environment of a plant is far from being a stationary equilibrium. Arising from the way our planet turns around its own axis and follows its orbit around the sun, all abiotic and biotic factors on its surface underlie oscillations over time and all forms of living organisms are forced to adapt to the local oscillations in their respective habitat in order to reach a lifespan of hours, days, weeks, months, years or decades and finally produce successful offspring. This is especially true of plants which being sessile, have evolved strategies to synchronize their internal processes with the external oscillations of their environment to their best advantage. This synchronization includes life cycle, developmental program, morphology, diurnal physiological rhythms (Somers et al. 1998; McClung 2006) and also uptake and assimilation of nutrients (Zhang et al. 1991; Bot and Kirkby 1992; Delhon et al. 1995; Haydon et al. 2011) on different timescales. A well-adjusted synchronization with the environment will increase the performance of a plant and increase competiveness. From this ecological and evolutionary point of view plants can be called "nutrient efficient", if they use the temporal and spatial availability of nutrients for an optimal and balanced vegetative and reproductive growth, which is most suitable to survive and compete in their respective habitat and niche.

In an agricultural context, however, the quality of the *intended outcome* shifts. Instead of offspring the plant produces a desired yield product, which can be utilized for food production and other economically relevant purposes. With agricultural practice and plant breeding to increase the production of this agronomic *intended outcome* the plant is detached from its ecological and evolutionary context. No longer exposed to the natural selection pressure but the artificial selection by man, plants are reshaped for agriculture: development, morphology and fluxes of resources are rerouted towards increased production of whatever yield is desired. Even after thousands of years of breeding, plants still bear their ecological heritage, which may conflict with agricultural interests and may limit the potential for traditional plant breeding to improve NUE. Bringing these two contexts together is one of the main tasks for plant scientists to understand the functioning of a plant in the semi-natural system of agriculture. In this way, ecophysiological potentials of plants might be further exploited for agricultural production and the limits for improving plants with traditional breeding might be identified and overcome. A profound understanding of the physiological background of NUE is the basis for modern plant breeding using molecular techniques.

In an ecological context, NUE can be examined at the level of individuals, populations, species, communities or entire ecosystems (Nardoto et al. 2006). NUE in agronomy can also be discussed on several levels (Fig. 1.1). On each level, input and output differ in kind, and different components have to be considered to adequately calculate the NUE of the respective system. In scientific discussions it is important to consider the same level to avoid confusion and misunderstanding. During the past few decades, scientists have become increasingly aware that agricultural systems can be regarded as ecosystems in which the role of soil composition and fertility, the influences of biotic interactions as well as abiotic environmental factors should not be underestimated. This is brought together in the concept of agroecology (Gliessman 1990; Schnug and Haneklaus 1998; Francis et al. 2003). In this holistic approach, not only the *intended outcome* but also the *input of costs* becomes very complex, as negative impacts of fertilisation, pesticides etc. have to be considered. In modern approaches many different benefits that an intact ecosystem delivers to society are assessed. These "ecosystem services"

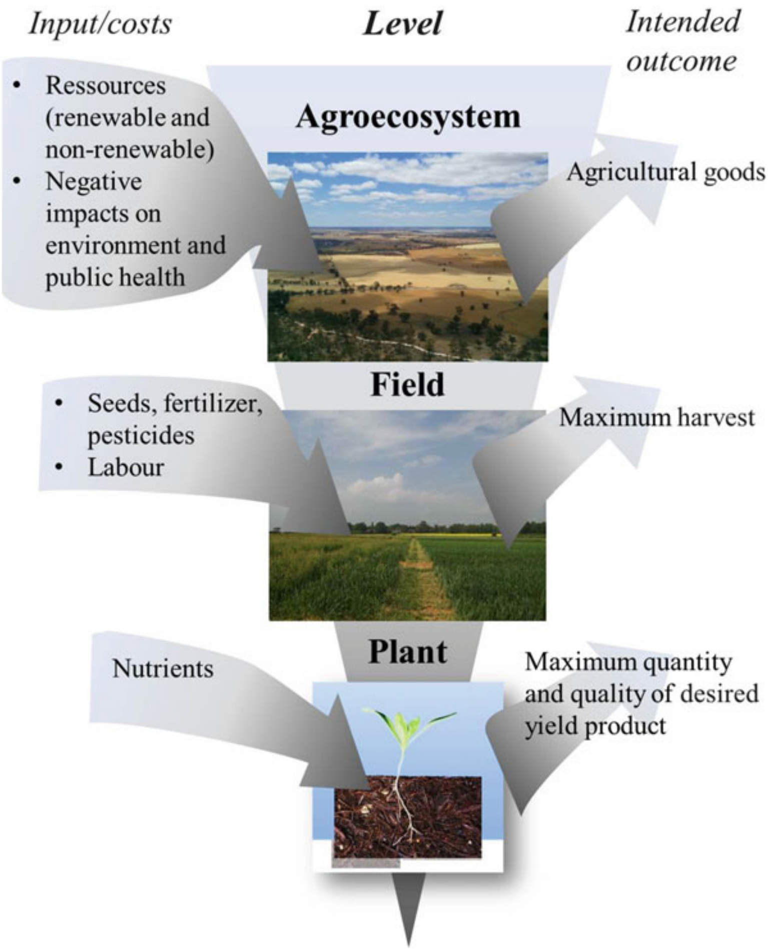

Fig. 1.1 NUE can be analysed and discussed on different levels of organization. On each level input and intended outcome differ in quality and a different terminology is used. Agroecologists regard the agricultural system with all associated ecosystems and society as the entity with a particular NUE, whereas agronomists put the field into focus. Plant physiologists deal with the plant as a complex input-output system with an inherent NUE. To avoid confusion in comparative research it helps to clarify on which level NUE is assessed

(Daily 1997) include delivery of agricultural goods as well as indirect beneficial properties such as the protective role of an intact forest against flooding or its capacity to purify water and bind carbon dioxide (Costanza et al. 1997; Daily et al. 2000; Tilman et al. 2002). Although it is difficult to assess the actual monetary value of all the components of an ecosystem, this concept is the only one that adequately expresses the efficiency of an agricultural system for a society in the long term by including all detrimental effects to the environment and to public health in the *input of costs* side of the calculation.

From the less holistic perspective of agronomy, the field is usually the level of choice for calculations of NUE. For farmers, the field represents an economic entity, where the inputs are the costs for labour and materials while the output is the harvest, usually measured by criteria such as “harvest index” (Donald and Hamblin 1976). In addition to NUE the term “fertiliser efficiency” is often used to describe how efficiently the applied fertiliser is used by the agronomic system: how much yield is produced, the quantity of nutrients which remains in the soil and how much is lost from the system by leaching and emission (Saurbeck and Helal 1990; Oenema et al. 2009). However, NUE can also be discussed at the plant level where a single plant instead of a whole field is regarded as an input-output system and in the present chapter we will deal with the individual plant and its NUE to discuss all the other dimensions and factors in relation to it. Improvement of NUE at the plant level also has the potential to improve NUE at higher levels and therefore has strong agronomic and environmental implications.

A common conceptual framework ensures a consistent use of terminology and definitions. As was noted above, NUE can be discussed in an ecological as well as an agronomical context. One context again can be divided into a sub-set of different levels of organization. By coming down to the level of an individual plant in an agronomical context, much of the universality of the term has been reduced. As already mentioned, the term *efficiency* implies the achievement of an intended outcome with a lowest possible input of costs. Therefore a very simplified definition for the efficiency of a given system can be expressed in the equation:

$$\mathit{Efficiency} = \mathit{Output}/\mathit{Input}$$

If values for input and output are competitive, the maximum value of efficiency is 1, in an ideal case where input equals output. Either decreasing the input or increasing the output might achieve higher efficiency. Every economical concept, which has to generate profit, in principle follows this simplified equation and agronomy is no exception. In all sectors of an industrialized economy it is desirable to make working processes less costly while maintaining or increasing the output. Technical innovation leads to more sophisticated techniques and methods, which also revolutionized the efficiency of agricultural practice at the field level. There is, however, an essential difference in improving an inanimate machine or process, which has been planned and constructed by man and improving a living organism such as a plant whose functioning is still far from being fully understood.

From a whole plant perspective NUE consists of several components and by regarding a plant as an input-output system, physiologists have established equations that put these components into context in relation to NUE. In the most universal approach, NUE at a plant level can be divided into two main components: the efficiency of nutrient acquisition (NAcE) and the efficiency with which the nutrient is utilized to produce the desired yield (nutrient utilization efficiency, NUtE):

$$NUE = NAcE * NUtE$$

While Chapin (1980) defined NUE simply as the inverse of the tissue nutrient concentration, NUtE can be further sub-divided into nutrient productivity (NP) and mean residence time, the period in which a certain nutrient can be used for production (MRT; Berendse and Aerts 1987). In the 1980s, Vitousek and co-workers (Vitousek 1982; Birk and Vitousek 1986) defined the nitrogen use efficiency (NitUE) of perennials as the amount of organic matter, which is lost from a plant or permanently stored in wood, divided by the amount of N lost or permanently stored. It was shown that NitUE of *Pinus taeda* L. stands decreased with increasing N availability. A more general definition was suggested by Berendse and Aerts (1987), who identified MRT and nitrogen productivity (NitP) as the main components of NitUE:

$$NitUE = NitP * MRT$$

According to Berendse and Aerts (1987), NitP describes the instantaneous rate of carbon fixation or biomass production per unit N present in the plant while MRT is a measure for the period in which N can be used for carbon fixation. This concept of MRT can theoretically be extended to other nutrients and plant species. In fertilisation models NP can be used to calculate the nutrient flux density that is necessary to maintain an optimal nutrient concentration in the plant (Ingestad 1988) but this again refers to the field and not to NUE at the plant level.

It is well known that plant species and ecotypes, which naturally grow in nutrient-poor soils possess mechanisms to increase the MRT of nutrients *e.g.* slow growth, high accumulation of nutrients and efficient remobilization of such storage capacities or a reduction of nutrient loss (Vázquez de Aldana and Berendse 1997). In soils where nutrients are available in excess or at least where nutrient availability is not the limiting factor, there is less selective pressure on developing such mechanisms. It is more important to have a high NP to grow fast and compete with neighbouring individuals for space and light and one way to reach this might be having a high nutrient throughput rather than a long MRT. Studies under controlled conditions with plants from both soil types showed that in the short term fast growing species were the better competitors in both optimal and limiting N conditions while in the longer term, plants from nutrient-poor soils outcompeted fast growing species under limiting conditions (Chapin 1980; Wedin and Tilman 1990; Berendse et al. 1992). It is considered that these differences in NUE between plants, which originated from soils with different nutrient concentrations, are due to differences in the underlying physiology, morphology and development. Van der Werf et al. (1993) showed how important morphological traits are for adapting NUE to the respective nutrient concentration in the soil. For instance, a high investment in root mass served for the high NP of fast growing species, though it should be noted that the majority of these studies on NUE dealt with wild species and N.

Expression of NP as unit biomass produced per unit nutrient may not always be the most suitable measure. The desired product in an agricultural system is not always biomass, consisting of structural or non-structural carbohydrates, but more often seeds that are rich in proteins or oil. It is thereby not only important how a nutrient contributes to growth but also how it improves the yield and quality of the desired product. Therefore, the respective nutrient can itself be a substrate for the production (*e.g.* as N and sulfur (S) for proteins) or a facilitator of the production (*e.g.* by being a component of an enzyme involved). Consequently NP on the basis of biomass may not always be the best measure and a more general indicator may be yield productivity (YP), which includes quantity and quality of the desired yield product per unit nutrient in the plant tissue. However, in agriculture and in general for all nutrients, NP (or YP) and MRT can be seen as sub-components of NUtE.

Physiological Processes Involved in NUE

After the derivation of a conceptual framework the key physiological processes involved in the complex trait NUE will be briefly summarized (Fig. 1.2). As described above, NAcE is one main component of NUE and consequently nutrient uptake is one of the key processes involved. Although some nutrients can be derived from the atmosphere (*viz*. N and S; Faller 1972; Stulen et al. 1998; De Kok et al. 2007), the plant largely depends on mineral nutrients taken up from the soil (Mengel and Kirkby 1987; Marschner 2012). These are either derived from weathering of parental rock material or biological breakdown of organic matter and the chemical availability to the plant depends on soil-specific properties which in turn determine the proportion of nutrients dissolved in the soil water (usually less than 0.2 %), bound to organic detritus (around 98 %) or adsorbed by soil colloids (Larcher 1995).

There has been much discussion on the significance of NAcE in explaining differences in NUE between plants. Most studies were focussed exclusively on N and came to different conclusions. For corn (*Zea mays L.*) it has been concluded from a study with different hybrids that NAcE is only relevant for differences in NitUE if the outside N concentrations are high, while NUtE of accumulated N was the driving variable if the supply was low (Moll et al. 1982). Whereas in pumpkin NAcE was not a possible target to improve NUE at either high or low N concentrations (Swiader et al. 1994). However, recent studies have suggested that an increased acidification capacity of the rhizosphere could be targeted to increase nitrate uptake and improve NUE (Paez-Valencia et al. 2013). In addition, the NUE of an agricultural system may be improved if plants could maintain internal nutrient concentrations and optimal growth with a lower outside concentration in the soil. Therefore understanding the response mechanisms of NAcE to nutrient deficiencies may improve the ability of crops to tolerate lower nutrient concentrations in the soil and thereby save fertiliser and reduce potential pollution.

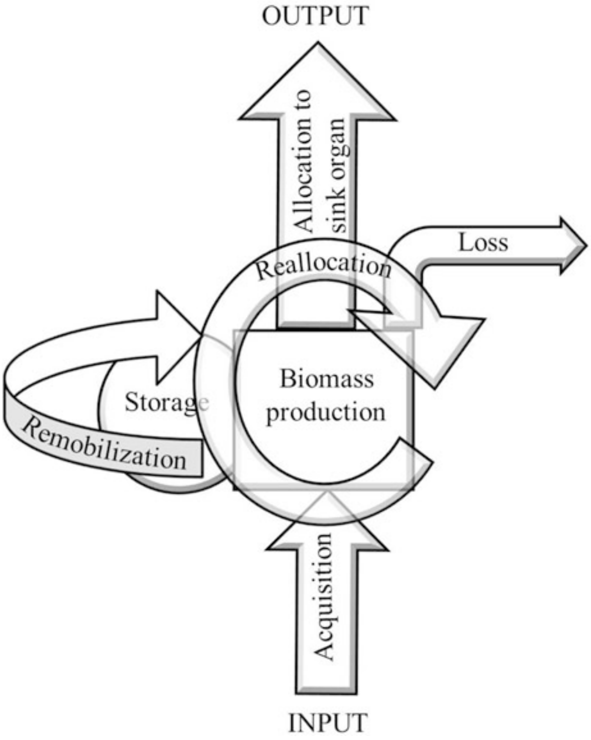

Fig. 1.2 Plant NUE has a complex physiological basis with interacting cellular and whole plant processes. After the acquisition of a nutrient it contributes directly or indirectly to the production of biomass and the final yield. Storage and remobilization are important processes that buffer asynchronies in nutrient demand and availability and the efficient reallocation of nutrients between different plant organs is a crucial process during plant development. Especially in cereals the translocation of nutrients to the finally harvested sink organ, the grains, is of particular importance. Nutrient loss can happen in several ways and displays a general constraint for NUE

Nutrient storage is another process of importance and can be functionally sub-divided into accumulation, reserve formation and recycling (Chapin et al. 1990). Accumulation summarizes the increase of compounds that are not directly related to growth. They accumulate simply because the availability exceeds the demand of the plant metabolism for these compounds. Reserve formation in contrast describes metabolically controlled storage in designated storage compounds. In this way compounds that otherwise would promote growth are stored in a form that does not. The formation of these storage compounds directly competes with growth and other processes that would use the compound in its original form as a substrate. In the process of recycling, compounds that originally contributed to growth promotion or other physiological functions but which would be lost are actively broken down to be used for future growth (Chapin et al. 1990). The significance of nutrient storage and remobilization for NUE depends on nutrient availability. A study with a number of hybrids of corn (*Zea mays L.*) revealed that under low N supply differences in NitUE between hybrids are related to variation in the utilization of stored N. However if N supply was high, acquisition efficiency became more important (Moll et al. 1982). A low ability to remobilize N leads to a lowered N harvest index in *Brassica napus* (Rossato et al. 2001). Similarly for S the limits of storage capacity and remobilization efficiency of sulfate are regarded as a constraint to NUE and a possible target for its improvement (Hawkesford 2000).

For biomass production plants convert inorganic carbon dioxide from the atmosphere to organic carbohydrates via photosynthesis. Fuelled by the energy of the sun, this process is the primary generator of all biomass on earth. Although N is most directly linked to photosynthesis, all the essential nutrients contribute in some form to growth promotion *i.e.* biomass production. This can happen directly if the nutrient is part of the carbon-assimilating apparatus or indirectly if it plays a role in energy transfer, defence, homeostasis, tolerance and other processes that facilitate optimal plant functioning. Consequently for every nutrient a respective NP can be assigned which is a measure for the biomass produced per unit of the nutrient in the plant. However, the mechanisms underlying this component of NUE and how the NP (and consequently the NUtE) of a certain nutrient can be improved are manifold and depend on the specific role that a nutrient plays in plant metabolism.

Again N is studied most intensively, and due to its direct link to photosynthesis and biomass production, there is a clear cut correlation with the NP of N and (i) the amount of total N invested in the photosynthetic tissue, (ii) the N efficiency of photosynthesis and (iii) relatively low loss of carbon due to respiration (Ågren 1985; Poorter et al. 1990). The carbon-assimilating enzyme Rubisco is currently one of the most prominent targets for possible genetic improvement of photosynthesis (Loomis and Amthor 1999; Parry et al. 2011), largely due to its apparent catalytic inefficiency in carboxylation and its consequent high abundance. The idea is that a higher efficiency would lead to less Rubisco being needed to maintain the same rate of photosynthesis and consequently, as this enzyme contains high amounts of N, a higher NUE of N. One intriguing approach is the attempt to express the Rubisco of some non-green algae, which have a greater specificity for CO_2, into higher plants (Whitney et al. 2001).

However, is the biochemical inefficiency of photosynthesis really the bottleneck that hinders higher biomass production and NUE? Although photosynthetic efficiency is in theory one of the key limiting factors for increasing biomass and crop yields (Long et al. 2006; Parry et al. 2011), supportive correlations in practice are not easy to assess and studies come to different conclusions. Studies on closely related germplasm of wheat showed a correlation of photosynthetic rate and yield (Watanabe et al. 1994), while comparisons of cultivated crops with their wild ancestors showed that the latter have a higher photosynthetic rate (Evans and Dunstone 1970). The potential limiting role of photosynthesis apparently depends to a greater extent on other processes with negative feedback on photosynthesis. If the capacity of the sink declines and the flux of photosynthates into sink products stagnates, this results in a compensating down-regulation of photosynthesis. Consequently the strength of the sink is just as important if not more so for yield as the efficiency of the source (Zelitch 1982; Borrás et al. 2004; Reynolds et al. 2005). According to these studies an increased sink capacity is required to increase photosynthesis and not the other way around. However, field studies with C_3 plant species under exposure to elevated levels of carbon dioxide (eCO_2) suggested that an increase in yield is, indeed source-limited or at least that sink capacity is stimulated by the increased source activity (higher net photosynthetic rate under eCO_2). These studies suggested that sink capacity is not necessarily a constraint to increase yield production by means of improving photosynthesis (Kimball et al. 2002; Ainsworth et al. 2004).

Apart from the question of how source and sink, or in other words supply and demand, determine and influence each other, the duality of photosynthesis and photorespiration makes the issue more complex. Up to one third of C fixed by the carboxylation activity of Rubisco is again lost by photorespiration. While some authors propose that photorespiration is of vital importance for plant functioning (Kozaki and Takeba 1996), others see these functions as at least partially redundant and suggest that a reduction of the C lost by this process would improve the efficiency of photosynthesis and biomass production (Long et al. 2006; Peterhansel and Maurino 2011). However, knowledge about the different roles of photorespiration in plant metabolism and NUE is still limited.

Another important process involved in NUE is the reallocation of nutrients. Re-use of nutrients from senescing leaves reduces nutrient loss and thereby increases NUE. Once more N is tightly coupled to C gain and its efficient allocation from one leaf to another contributes to optimal C fixation (Field 1983). In this process older leaves with declining photosynthetic N efficiency are exploited as a source for N, which is reallocated to young leaves to promote their growth. In this way N is used efficiently for photosynthesis at a whole plant level (Westoby et al. 2002; Escudero and Mediavilla 2003) and also NUE is increased, as loss is reduced. Resorption of nutrients from senescing leaves has also been studied for P (Lajtha 1987; Chapin and Moilanen 1991; Killingbeck 1996). It is generally assumed that the costs of this process are very low for the plant (Givnish 2002), which further supports reallocation of nutrients as a key process for the improvement of NUE. However, nutrients, which are efficiently recycled within the plant and thereby are not lost during senescence, will also not end up in the decomposition cycle in the soil. Whether this has negative feedback consequences for the plant and NUE is not fully understood and much will depend on the particular system. However, there are speculations about a general trade-off between efficient nutrient re-sorption in plants and the decomposability of litter (Aerts 1997).

The translocation of nutrients to the harvestable yield organ follows the same principles as the allocation to other plant organs. For obvious reasons it is, however, the most crucial allocation process for yield production and therefore regarded as a special case that is worthy of additional attention. Plant breeding has resulted in a wide diversity of crops in which virtually any part of a plant might serve as a yield organ: roots, stems, leaves, seeds, fruits. However, the six most important crops in terms of worldwide food and feed production are all grain crops (corn, rice, wheat, soybean, barley and sorghum) with seeds being the plant organ of interest and grain filling as a crucial step for yield production (Borrás et al. 2004; Foulkes et al. 2011). The reallocation of N from senescing leaves to the developing seeds is of particular importance in determining the quality of the crop and thus increasing the efficiency of reallocating N from leaves to grains is a potential target for improving NUE

(Barbottin et al. 2005). While N translocation to grain determines its quality, on improving NUE of P could be achieved by decreasing its translocation to the grain (Rose et al. 2010). Additionally it should be noticed that the efficient translocation of nutrients (as well as C) to yield organs is not only determined by the efficiency of the exploitation of the sink organs but also by the sink strength (*e.g.* for wheat: Reynolds et al. 2005; for rice: Ntanos and Koutroubas 2002).

The loss of nutrients to the outside may be the most obvious constraint to NUE. There are several paths by which nutrients can be lost by plants to their environment. Leaves lose nutrients by leaching, in some cases as gases or other volatile compounds (Eichert and Fernández 2012) and finally by litter fall, *i.e.* senescence. These processes of nutrient loss can either be a way for the plant to balance its nutritional status or may be unavoidable, for example due to wash-off by rain or evaporation due to a trade-off with stomatal conductance. In the latter case, a reduction of nutrient loss from the plant to its environment before harvest may be a target for the improvement of NUE, particularly in crop systems where litter and its nutritional status play a minor role. Further research is required to more fully understand the physiological significance of these losses in order to distinguish between avoidable leaks and metabolic valves, which assure internal nutrient balance and thereby optimal plant functioning.

Factors Affecting NUE

The complex physiological basis of NUE becomes even more complex in reality, as the contribution of these processes is modified by numerous factors, which can be categorized into plant, environment and nutrient (Fig. 1.3). Numerous studies and reviews have pointed out that concrete definitions of NUE depend to a great extent on plant species and growth type. Again it should be stated that NUE is an artificial term based on a hypothetical input-output concept. The diversity of NUE in nature, however, reflects the diversity of plant strategies to survive and produce successful offspring in their very different niches. How they perform if we apply the agricultural standard of NUE does not reflect their ecological and evolutionary fitness. Despite breeding the strong influence of the respective phylogenetic background of a cultivated plant on its performance and peculiarities in the field adds another degree of difficulty when defining one general concept for NUE. Fundamental differences between crops can be metabolic in nature, *e.g.* between C_3 and C_4 plants (Brown 1978) or arise from different growth forms such as trees which are harvested after decades, and herbaceous crop species which produce their yield within months. Processes such as nutrient storage and reallocation function very differently and have different significance for NUE in annual and perennial species (Aerts and Chapin 1999), as well as in deciduous and evergreens (Chapin and Kedrowski 1983; Aerts 1990; Franklin et al. 2009). This variability in plant growth strategy makes it hard to derive one concept and set of definitions for NUE and its

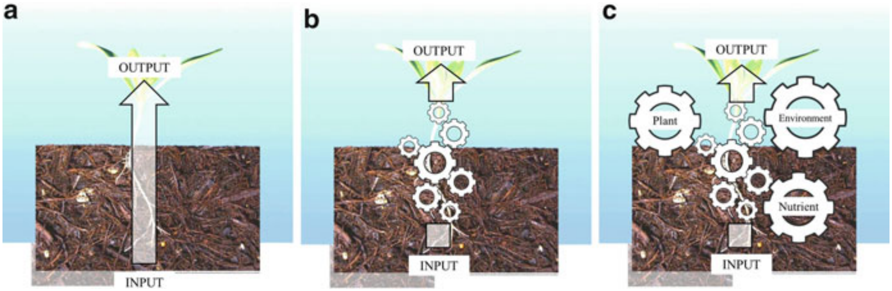

Fig. 1.3 The complexity of NUE – In an agronomical context the plant is regarded as an input-output system with an inherent efficiency that shall be improved (**a**). Numerous physiological processes are determining the NUE of a plant (**b**) and the actual contribution of each process to the NUE of the plant is biased by many factors of the three variables plant, environment and nutrient (**c**). To develop strategies for the improvement of NUE in an agricultural system both the physiological processes involved and the factors that influence their contribution to NUE have to be considered

improvement for all species (and even cultivars). To identify the physiological processes whose modification could increase the NUE of a respective crop, the particular characteristics should be carefully taken into account and adequate comparisons of NUE are often only possible within cultivars or strains of the same species. However, the repertoire of physiological strategies in nature can also serve as a pool of mechanistic possibilities to improve NUE, *e.g.* by transferring beneficial traits within distantly related species via transgenic methods.

Another plant-specific variable is the kind of yield the crop will produce. As described in the introduction the *intended outcome* in agriculture is a maximum quantity of yield. However, the specific NUE and the way to improve it will differ fundamentally depending on the desired yield *quality*. The relevance of the physiological processes described above for NUE shifts completely if the desired yield is starch or sugar and not proteins or oil. While for the former efficient biomass production and C storage will be important, for the latter allocation to the seeds increases in relevance. Furthermore, virtually all morphological parts can be the yield organ into which the desired compounds are allocated before it is finally harvested.

Environment is the second variable that has an important impact on NUE. According to Evans and Fischer (1999) yield potential (Yp) can be defined as 'the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting, and with pests, diseases, weeds, lodging and other stresses effectively controlled'. The yield of a crop depends largely on the environmental conditions during the growing period. Nutrients are not always the limiting factor for plant growth and crop yield. Environmental factors such as temperature, light and rain or soil-specific factors such as soil composition, pH or pollution with salts or heavy metals may also be of great significance. If this is the case, there are more urgent steps to be taken to increase productivity than increasing NUE (Boyer 1982). Even if nutrient availability is the limiting factor, the physiological processes that are involved in NUE may be modified by environmental conditions. For instance, drought has numerous implications for the mineral nutrition of plants. As the uptake of many nutrients is depending on the mass flow of water there is a direct relationship between water availability and the uptake of mobile nutrients such as nitrate (Smika et al. 1965; Buljovcic and Engels 2001). In turn, an optimal N supply was shown to alleviate detrimental effects of drought in *Zea mays* (Zhang et al. 2007). However, not only the uptake but also the translocation to the shoot via the xylem is impaired during drought stress, which may affect all nutrients but which has been shown for P (Rasnick 1970). Even moderate drought stress might cause P deficiency in crops, which is an explanation for the often-observed positive effect of increased P fertilisation under dry conditions (Turner 1985; Garg et al. 2004).

It is known that growth rate and the uptake of certain nutrients (*e.g*. P but not N) may show a strong decline under low light compared to high light conditions, if the nutrient supply is adequate (Bloom 1985; Chapin 1991). The same is true for both low and high temperatures (Tindall et al. 1990). This dependency of growth and nutrient uptake on temperature and light leads to a different relevance of these processes for NUE in different patches of a field, during different seasons and in different climatic regions of the world.

The mineralization and cycles of essential nutrients such as N are mainly driven by the properties of the soil. Litter decomposition plays a crucial role in overall nutrient cycling in an ecosystem as well as in an agroecosystem. Globally the extent of litter decomposition depends mainly on temperature, while on a regional scale the chemical composition of the litter becomes most important (Aerts and Chapin 1999). In this way the soil not only plays a crucial role in the NUE of a field or a whole agroecosystem but also at plant level where NUE is partly governed by soil specific factors. Nutrient uptake is the process, which is affected most obviously. In natural ecosystems nutrient uptake is ultimately dependent on the nutrient supply rate by the parental rock material. Its mineral composition, age and weathering rate determine the nutritional status of a soil (Lambers et al. 2008). In an agricultural system the nutrient composition of the soil is mainly controlled by fertilisation. However, there are other factors with an impact on nutrient uptake, which are usually under much less control. One is the pH of the rhizosphere, which has a tremendous impact on the ability of the plant root to acquire different nutrients. In addition the soil is much more than just part of the plant's *abiotic* environment. It hosts a still widely unknown diversity of microbial life. Interactions with arbuscular mycorrhiza and rhizobacteria that increase the uptake surface of plant roots and provide nutrients to it may alter the NUE of crops, increase yield significantly and improve fertiliser management on a field scale (Smith et al. 1992; Adesemoye et al. 2008; Adesemoye and Kloepper 2009).

While the below ground part of the plant is surrounded by soil, the above-ground part is exposed to the atmosphere and although almost 100 % of its volume is equal in composition around the globe, there are traces of gases which fluctuate in their local concentrations (Kraus 2006). Some of these gases can have a significant impact on plant metabolism. Most of these N- and S-containing gases are usually referred to as pollutants, as they originate to a great extent from anthropogenic activities but also from volcanic activities. It has, however, been shown that some of these gases have an ambivalent mode of action on plants, as they are not only toxic if too high in concentration but can also serve as nutrients (De Kok et al. 2002, 2007). This can either happen by wet deposition, *i.e.* a deposition to the soil by rain, or by dry deposition via the stomata of plants. This additional nutrition from the atmosphere and predictions for changes in the concentration of these gases should be included in future calculations of NUE and fertilisation regimes.

The third variable that complicates efforts to define one general concept for NUE is the nutrient itself, as nutrients differ not only in their physiochemical properties but also in their uptake by and function in the plant. For each of them, the relevance of the underlying physiological processes for NUE differs and so do the necessary strategies for the improvement of NUE. For one nutrient the capacity of storage might be crucial, while for another the uptake or the allocation to the sink organ limits production. For this reason, studies on NUE in which different nutrients are used are often difficult to compare. More specific definitions and components have to be developed to accommodate this diversity. A recent study suggested three components for NitUE: N uptake efficiency, grain-specific N efficiency and grain N concentration (Weih et al. 2011). S for example is involved in plant defence and thereby using less S while maintaining the same defence status should increase S use efficiency. Some micronutrients are co-factors of particular enzymes so consequently a higher efficiency and decreased amount of these enzymes could increase the NUE of these micronutrients. Furthermore, some nutrients are of nutritional value, which again increases the relevance of translocation to the yield organ, *e.g.* the grain, while other nutrients are not desired to be part of the yield but play a role in its production. Conclusively the NUE of a given nutrient depends on its importance for yield production and its value for human nutrition, *i.e.* its concentration in the yield. Each case needs a different set of strategies for an improvement of NUE.

Improvement of NUE

Although controlled by man, agriculture remains a semi-artificial environment, which is still subject to oscillations, particularly from outside the agroecosystem. These oscillations may be entirely different from those in the ancient, natural habitat of the plant species and thus transferring it to an agricultural system may lead to sub-optimal growth and yield. Since the beginning of agricultural practice (ca. 11,000–13,000 years ago; Allard 1999) farmers have tried to solve these problems with two different approaches:

(i) By reducing the amplitude of environmental oscillations either by growing plants only in a certain season to avoid extremes in weather (*e.g.* cold winter, dry summers or rainy seasons) or by creating more stable conditions in the field (*e.g.* by using hedges as wind protection and digging moats to avoid flooding or, in modern times, building partially closed and controlled environments such as greenhouses).

Another important factor is the nutrient content of the soil, which was controlled by deploying manure before the revolutionary discovery of Liebig's law of the minimum and the advent of modern fertilisers. (ii) By reducing all kinds of unfavourable dynamics and traits in the plant's phenotype, which are relics of adaptation to its ancient habitat and/or part of its developmental program but no longer needed in cultivation. This is done by breeding, which makes use of the same mechanisms as evolution (variation and selection). Plants are selected for traits of agricultural interest with a main focus on bigger sink organs and higher concentrations of the compounds of interest at the expense of traits and adaptations that are no longer necessary.

In theory a combination of (i) and (ii) could result in a stable farming system in which environment and plant are under full control and no unfavourable oscillations and dynamics should occur anymore. Nutrient loss from the system would be at a minimum resulting in an optimal input-output ratio. The result would be to equal out all the variables that make NUE such a complicated trait: plant, environment and nutrient specific factors (see above). In reality, however, this is an ideal scenario and is presently far from being achievable. First, the technological effort to control all environmental factors and their respective oscillations is uneconomical and second the complex ways in which plant functioning is still largely unknown. Consequently the compromise that has developed over thousands of years of plant domestication is the attempt to synchronize the oscillations of environment and plant as well as possible. This is especially true for fertilisation because the discrepancy between demand of the plant and availability of nutrients in the soil is an important factor that can hinder optimal growth. Nutrient storage can buffer this discrepancy only to some extent and matching nutrient supply by fertiliser application to plant demand is regarded as one of the most promising ways to reach higher fertiliser use efficiency (Cassman et al. 1993; Frink et al. 1999; Tilman et al. 2002).

Without a deeper understanding of the biochemical and physiological processes involved, traditional breeding managed for more than 10,000 years of agriculture to develop plants with massive yield organs containing high protein, starch or oil content, compared to their ancestors (Mazoyer and Roudart 2006). At the same time major steps towards increasing output-input-ratios have been made by the progress of agricultural practice, technology and science (Russell 1966; Thompson 2011).

With Liebig's postulation of the "law of the minimum" (see review Browne 1942) and its resolution in terms of N supply by industrial production of relatively cheap nitrogenous fertilisers (mainly by the Haber-Bosch process in which N and hydrogen are directly converted to ammonia, see *e.g.* Tour 1920), the modern age of agriculture began and led to a historical change of paradigms, also named the "Green Revolution" (Borlaug 1972). Instead of trying to have an optimal input-output ratio, as it is necessary if fertiliser is a rare commodity, the highest possible output became the primary aim and remains so in present agricultural practice. The increased growth of cereals due to super-optimal N supply led to another factor becoming a major constraint for yield, namely the damage caused by lodging. The solution was the breeding of "dwarf cultivars" of wheat and rice in the 1960s by deployment of dwarfing genes. This in turn was only possible with better weed control through the development of herbicides so that the smaller cereals were not overgrown by wild weeds. This innovative trinity of the Green Revolution made it possible to neglect the input-output ratio and exclusively focus on maximum output (Evans 1998). As a result, yield per hectare increased tremendously during the last century and enabled an explosion of human population counting billions instead of millions. However, it has become more and more apparent that this practice cannot continue in the future. Parallel to a linear increase of global yields since the 1960s, the NUE of agricultural system (measured as unit yield per unit fertiliser applied) continuously declined. This "law of diminishing returns" implies that further increases in fertiliser application will not lead to higher yields in the same proportion as in the past (Tilman et al. 2002). High levels of nutrient input have resulted in pollution of the environment on the one hand and anticipated shortages of non-renewable resources such as inorganic P on the other. Furthermore, the benefits of these high outputs are very unevenly distributed over the world and with some production wasted in Europe and North America, spikes in food prices and hunger crises are expected to occur more frequently in developing countries. The awareness of this alarming trend led policymakers to put "food security" on the top of political agendas and consequently also into scientific focus (Rosegrant and Cline 2003; Vitousek et al. 2009; Godfray et al. 2010; Hawkesford et al. 2013).

To some extent the agriculture of the future has to come back to the old paradigm of requiring a more optimal input-output ratio. However, maintenance of the ongoing trend of increasing output in form of yield is an imperative due to the still-growing world population and no concept, which reduces the output, can be realistically considered (Evans 1998). Consequently, modifications of the input-output ratio have to concentrate on the input side of the equation. At field level (Fig. 1.1) the approaches to improve the input-output ratio may be categorized in two dimensions: time and space. This is again based on the general conception of plant and environment as two non-stationary, heterogeneous and oscillating systems. The supply with nutrients (fertiliser) can be adapted to the need of the plant for growth over time to lose fewer nutrients from the system in times of a low crop demand and to avoid concentrations being too low if the demand is high. In addition, nutrient supply and its demand in the field are not homogenously distributed in space but instead graduated or patchy. A homogenous application of nutrients thereby leads to excess supply in some parts of the field, resulting in nutrient loss, and to a sub-optimal supply in other parts, resulting in a non-optimal growth and yield. For both dimensions technological innovations have been developed, commonly summarized with the term "precision agriculture" (Pierce and Nowak 1999; Stafford 2000; Zhang et al. 2002). However, in addition there might be ways to breed or genetically manipulate the plant in a way that it uses nutrients more efficient and consequently produces the desired yield with less nutrient input. While transgenic and genetic techniques offer the possibility for accelerated improvement through genetic modifications and marker assisted breeding, whole plant physiology provides the knowledge to use these tools in an effective way. To practically improve the NUE of a plant in a particular agricultural system, the relevance of the underlying physiological processes (Fig. 1.2) has to be analysed in relation to the variables that modify it (Fig. 1.3). Once the limiting processes are identified, breeding or transgenic methods might lead to further improvement of NUE. For success, the physical and physiological trade-offs that limit an improvement in NUE have to be identified. This will be the topic of the last part of this chapter.

NUE – Challenges from a Whole Plant Perspective

As stated previously, NP and MRT can be seen as sub-components of NUtE. Consequently both could be targeted to improve NUE in cropping systems. Berendse and Aerts (1987) have pointed out the apparent ecological trade-off of NitP and MRT. While in nutrient-poor soils a long MRT is favourable, a high NitP gives advantages in nutrient-rich soils. Plant species in nutrient-rich soils generally possess a larger photosynthetic apparatus and can thereby rapidly make use of higher N availability, while species in nutrient-poor soils are able to use spare nutrients more economically. Theoretically, generalist species should combine both traits, but evidence suggests that they are competitive (Berendse et al. 1987). A later study on species with different life forms in a sub-arctic environment confirmed this negative relationship of NitP and MRT (Eckstein and Karlsson 1997), and others followed (Yasumura et al. 2002; Silla and Escudero 2004). Within the same species, this trade-off also appears to be consistent, with higher N supply leading to higher NitP but lower MRT (Yuan et al. 2005) or the other way around (Yuan et al. 2008). High nutrient supply, however, may even lead to a decline of both components in certain circumstances. A decline in NP can be caused by cross- and self-shading and an accompanied decrease in photosynthetic activity and a lower MRT can be the result of enhanced litter production or leaching (Meuleman et al. 2002).

As studies have almost exclusively focused on natural systems, perennials and N, it is difficult to assess if a strict trade-off between NP and MRT exists in agricultural crops and for all nutrients. As litter decomposability is not an issue in annual crop production, a high NP and long MRT at the same time are desired to maximize yield output and minimize nutrient input. The fact that traits, which lead to either a high NP or a long MRT, are not co-occurring in nature does not necessarily mean that breeding could not combine them. More integrated research on the described underlying physiological processes and their possible trade-offs are needed, including research with nutrients other than N.

In general, NUE is only studied for one single nutrient. There are few studies, which address the question whether improving the NUE for one nutrient will affect the NUE of others. Given the interactive and competitive nature of nutrients in many physiological processes, it seems likely that increasing NUE for one nutrient will also alter the NUE of others in a positive or negative manner.

On the level of nutrient uptake from the soil there are manifold co-influences known, but their whole extent is still far from being understood. Many of these are caused by the charged nature of ions when dissolved in water. If, for example, N is taken up predominantly as positive charged ammonium, the uptake of other cations such as magnesium and calcium is impaired, probably in order to maintain a balance of charge (Haynes and Goh 1978). On the other hand, plants that are supplied with nitrate absorb less phosphate than plants supplied with ammonium (Riley and Barber 1971). Similarly, do sulfate or nitrate show a higher accumulation in the plant if the other is missing in the root medium (Steingröver et al. 1986; Koralewska et al. 2009), either due to a replacement as an osmolyte in the vacuole or to a balance of anion-cation uptake, *i.e.* a balance of charge. This is a hint that increasing the storage capacity of the vacuole for one nutrient could decrease the capacity for others of the same charge. Interactions of the uptake of nutrients with different charge have been observed, for example for sulfate and iron (Paolacci et al. 2013). Here a direct interaction on the level of uptake does not seem likely. In contrast a higher uptake of sulfate under iron deficiency is suggested to serve for the production of S-containing defence compounds and a coupling of both nutrients could be due to their combination in Fe-S clusters (Forieri et al. 2013). Another example of the interactive effects of the uptake of different nutrients has been shown for sulfate, nitrate and ammonium (Clarkson et al. 1989) and there are many more reported. The direct linkage between the uptake of different nutrients, however, is under critical discussion. Studies in which plants were exposed to an atmospheric S source while deprivation occurred in the rhizosphere show an apparent uncoupling of sulfate and nitrate uptake (Westerman et al. 2000, 2001; Stulen and De Kok 2012).

Another potential conflict in the uptake of different nutrients arises if they use the same uptake system. This may be true, for instance, for the transport of phosphate and sulfate across the chloroplast membrane, which was reported to be competitive (Gross et al. 1990). As well as Liebig's "law of the minimum" states that identifying and increasing the amount of the most limiting factor can increase plant production, there is the far less popular but equally important "law of the optimum" formulated by Liebscher (see review Browne 1942). It states that the increase of such a limiting factor contributes more to the productivity of the system, the closer all other factors are to their optimum. Liebscher studied N, P and K nutrition of crops and was one of the first researchers to demonstrate the strong interactive component of different nutrients and their contributions to yield. It does not contradict Liebig's "law of the minimum" but shows that reality is more complex. Improvement of NUtE for any of the three nutrients N, P and K requires a balanced supply with the other two (Janssen 1998).

An important question for the future improvement of plant NUE is whether interferences with other efficiencies exist, especially if those turn out to be real physical trade-offs. Such trade-offs usually arise from the involvement of physiological mechanisms in several efficiencies. Studies on different tree species showed intraspecific inverse relationships between water use efficiency (WUE) and NitUE (Field et al. 1983; Reich et al. 1989), which appear to explain the spatial distribution of species on either N-poor or water-deficient soils (Patterson et al. 1997) but also have implications for the improvement of NUE in agriculture. This trade-off has stomatal as well as non-stomatal components (Reich et al. 1989) depending on the water and N status of the soil. How relevant it is for agricultural practice and crop breeding towards an increased NUE has still to be clarified. It might help the case to distinguish between the levels of NAcE and NUtE. If water is a limiting factor during crop growth, NAcE usually increases in its relevance, as nutrient uptake is physically coupled to water uptake. Climate change may mean seasonal droughts appear more frequently in many regions of the world which further increases the need for crops with a high WUE (Reynolds et al. 2011). For wheat, for example, it has been shown that under water limiting conditions genotypes with a greater root biomass produce more grains, probably due to both a high WUE and NAcE during early growth due to enhanced ability to capture water and reduce nitrate leaching (Ehdaie et al. 2010). Root traits are considered as a selection criterion especially under drought conditions (Ren et al. 2012) but there are strong interactions with NAcE that have to be considered. For example, the responses of root architecture to P and N deficiency are very different. While P deficiency leads to a shallow root system, foraging for the immobile phosphate, N deficiency causes a deep, scarcely branched root system. The latter is also associated with an efficient capture of water during periodical drought (White et al. 2013) implying that the NAcE for N and an efficient water uptake are not in competition but share a similar morphological trait. How the shallow root system that leads to a higher NAcE of P displays a constraint to WUE needs to be further evaluated. However, there are also reports that show an apparent negative interaction of N supply with WUE. High N supply leads to an inhibition of the typical growth characteristics that lead to a higher WUE in *Sophora davidii* while appropriate or low supply alleviated drought stress (Wu et al. 2008).

NUtE, NitUE and WUE show strong interactions due to their correlative effects on stomatal conductance, gas exchange and photosynthesis. In wheat, a higher N supply is reported to lead to an increase in WUE but at the same time to a decreased NitUE (Shangguan et al. 2000; Cabrera-Bosquet et al. 2007). This trade-off between NUtE and WUE is particularly noticeable if the N-to-grain price ratio in an agricultural system is high (Sadras and Rodriguez 2010). How the NUE of nutrients other than N interferes with WUE is still an open question.

Other studies have revealed a trade-off between N and light use efficiency (LUE) in canopies (Niinemets and Tenhunen 1997; Hirose and Bazzaz 1998). This can be explained by the fact that a high concentration of N in leaves leads to a high LUE but low NitUE. The impact of this trade-off again depends on the factors described above. It becomes more relevant under shading conditions and for trees because the build-up of the desired timber strongly depends on exploiting light efficiently during the growing season.

Again, it should be noted that inverse relationships between certain plant traits observed in nature do not necessarily display real physical trade-offs that cannot be overcome in plant breeding. They might just reflect genetic adaptations to different habitats or an ecological disadvantage of the combination of both traits (Veneklaas et al. 2012). If this is the case traits, which never occur together in nature may still be combined in one crop.

Finding plant traits, which improve Yp and NUE is a major aim of modern breeding programs. The genetic variability of crops, as well as of the model plant *Arabidopsis thaliana*, may serve as sources of diversity and promising traits may then be incorporated into transgenic crop plants. Additionally future techniques might enable the transfer of physiological traits such as C_4 metabolism (Leegood 2002) or N fixation (Charpentier and Oldroyd 2010; Beatty and Good 2011) between distantly related species. In this way, ecological but non-physical trade-offs could theoretically be overcome faster, and crop plants could be complemented with physiological properties that they would never gain through breeding. The diversity present in nature is potentially a rich source of traits that could improve the NUE of crops. There may be plant species that evolved mechanisms to use nutrients much more efficiently than crops but which science has yet to exploit. In particular species from nutrient-poor habitats are very promising candidates. Thus transgenics could be a useful tool to engineer crops whilst ecophysiology delivers the ideas of how these modifications will look.

Conclusions

Plant NUE is as complex and multi-dimensional as the plant itself. Consequently the greatest challenge, but also the greatest opportunity for modern plant nutrition research, is the integration of various disciplines and approaches. Use of state-of-the-art methods in transcriptomics, metabolomics, and proteomics give researchers unprecedented opportunities to obtain huge amounts of information with high resolution (see the other chapters of this book), not least enabled by the exponential increase of computing performance since its emergence (Moore 1975; Kurzweil 2001). The growing understanding of complex molecular networks and their holistic responses to alterations in nutrient availability contributes to uncovering the genetic basis of NUE and shows how complex metabolic pathways are interacting on a molecular level. However, the real power of molecular techniques for future crop breeding can only unfold if the complexity of the underlying physiological processes and their contribution to NUE is to be further understood.

Additionally there are physiological trade-offs that challenge the improvement of NUE. It might be possible to overcome some of them by modern molecular breeding techniques; others might be physically determined and display a real limit for the improvement of NUE. Further investigation is necessary to determine the physiological basis of these trade-offs before tools such as genetic manipulation may be used to overcome them. As studies on NUE usually focus on only one nutrient (and usually only N or P), there is little data available on possible trade-offs between the NUE of different

(continued)

nutrients. However, the compensatory and interactive nature of the uptake and storage of different nutrients suggests that such inter-nutritional trade-offs could exist. Adding to this complexity is the knowledge that all these possible trade-offs are strongly influenced by environment, plant and nutrient specific variables.

In conclusion, the physiological basis of NUE still displays a wide field for future research and the complexity and plasticity of plant metabolism may yet have many surprises in store in our attempts to “improve” it. More integrative studies, connecting several scientific disciplines are required to understand the complexity of all the variables that influence NUE resulting in physiologically relevant strategies for the improvement of plant NUE in agricultural production.

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