Chapter 10
Nutrient Use Efficiency

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Abstract Much of the recent gains in global crop production have been underpinned by greater use of fertilizer, especially nitrogen and phosphorus, and continued improvements in plant nutrition will be needed to meet the increasing demands for food and fiber from a growing world population. Climate change presents many challenges to improvements in nutrient use efficiency by its direct effects on the growth and yield of plants, and hence on nutrient demand, and by its influence on soil nutrient cycling, nutrient availability, and uptake. However, the consequences of climate change on plant nutrition are difficult to predict because of the complexity of the soil–plant–atmosphere system. Empirical data suggests that enhanced as well as reduced nutrient availability and uptake may occur as a result of climate change, depending on the nutrient in question and the component of the climate that changes. Notwithstanding the uncertainty of the effects of climate change on soil nutrient availability and plant nutrient uptake, improvements in nutrient use efficiency will be required to sustain productivity into the future.

Over significant areas of the world's arable land, high inputs of nutrients have increased soil nutrient reserves and fertilizer use efficiency is low, while in other

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regions, impoverished soils and low rates of fertilizer use have limited the capacity of farmers to provide adequate amounts of nutritious food. Developing varieties with enhanced nutrient use efficiency provides a way of improving productivity in both situations, although the traits that are targeted may differ. The two pathways by which nutrient use efficiency can be improved are by better uptake efficiency or by enhanced utilization efficiency. The relative importance of these strategies will reflect the amount and availability of nutrients in the soil. Genetic variation in nutrient use efficiency in plants is well documented, but improvements in nutrient use efficiency in the major food crops so far have been modest. Reasons why progress has been limited include inconsistent and sometimes confusing definitions of nutrient use efficiency, incomplete understanding of the genetic and physiological bases of differences in nutrient use efficiency, lack of field validation of assays, and little consideration of genotype × environment interactions in the expression of nutrient use efficiency. However, currently a powerful array of molecular and genomic techniques promises considerable advances in understanding nutrient use efficiency and developing varieties that are more nutrient efficient. Combined with traditional disciplines of plant breeding, crop physiology, and agronomy, new opportunities are developing to study genetic differences in nutrient use efficiency and to allow agriculture to meet the challenges of increased production of quality grain in a variable environment.

10.1 Introduction

The changes in climate that are predicted to occur during the next century present many challenges to sustainable crop production and food security. A burgeoning world population accompanied by increasing standards of living will require unprecedented levels of production of food, fiber, and industrial crops. This needs to be achieved with little further increase in the area of arable land and with finite and increasingly expensive supplies of fertilizer. Greater productivity needs to occur at a time when large areas of the world's agricultural land will experience increases in the frequency and severity of heat stress and drought (IPCC 2007; Handmer et al. 2012). Improvements are also needed in the nutrient content of the major stable food crops to alleviate the chronic nutritional problems that occur in many countries, but particularly in developing countries (Graham et al. 2001, 2007).

These challenges have brought the importance of plant nutrition to sustainable agricultural production into sharp focus and have highlighted the need to improve nutrient use efficiency (NTUE). The higher yields that will be required to maintain (or improve) food security will require increased uptake of most of the essential nutrients at a time when shortages of some fertilizers are being predicted (Cordell et al. 2009).

Most agricultural soils are deficient in one or more essential nutrients or have other nutritional constraints to yield (Lynch and St. Clair 2004). The substantial increases in global grain production that have occurred up to now have been based, in part, on improvements in crop nutrition. However, successes of the past are no guarantee for future improvements. It is acknowledged that the yield improvement that was associated with using increasingly high rates of fertilizer has led to rates of nutrient input in excess of crop requirements, leading to low NTUE, a waste of input of nutrients, and reductions in soil and water quality in many regions of the world (Vitousek et al. 2009). On the other hand, there are still regions of the world where chronically low soil fertility is limiting agricultural production. Improvements in NTUE will rely on identifying weaknesses in current production practices and correcting past failures, as well as developing novel approaches to improve nutrient supply and nutrient efficiency.

Despite the central role of plant nutrition in sustaining the productivity of agricultural systems, the effect of climate change on nutrient availability and uptake has received little consideration. Attention has focused on breeding for tolerance to heat and drought resistance and only brief mention is made about crop nutrition, and then comments are confined largely to nitrogen nutrition (Reddy and Hodges 2000; Semenov and Halford 2009; Reynolds 2010; McClean et al. 2011; Olesen et al. 2011). Balanced nutrition of crops is not only important in its own right, but maintaining an adequate level of crop nutrition is also important to help plants cope with biotic and abiotic stress (Huber and Graham 1999; Cakmak 2000; Walters and Bingham 2007; Cakmak and Kirkby 2008). Consequently, the productivity and resilience of crop production in the face of changes in climate will be linked to the ability to maintain the nutritional health of crops and to enhance the NTUE of the cropping system.

There are two approaches to improving NTUE: using crop management to improve the supply and efficiency of nutrient uptake and its conversion to a harvestable product, and improving the ability of crop plants to take up and use nutrients from the soil and fertilizer. The two approaches are complementary and substantial gains in the NTUE of a farming system are likely to come when both strategies are used. We have witnessed the effect of combining variety improvement with fertilizer use in the past when high yielding varieties of crops allowed higher rates of fertilizer (and other inputs) to be applied, leading to large increases in productivity, which also resulted in an increase in NTUE (Ortiz-Monasterio et al. 1997).

The effects of climate change on productivity will be variable and will be influenced by the ability of farmers to adapt to a changing environment. This will be affected not only by their financial resources, and access to information and technology but also their perception of risk and the foibles of human decision making (Lobell and Burke 2010; Hayman et al. 2011). Growing a new variety with superior traits is frequently a low-risk investment and farmers readily adopt new varieties if they perceive a benefit in doing so. Modern high-yielding varieties have been widely adopted in developing countries because they have increased yields and yield stability (Maredia et al. 2000; Renkow and Byerlee 2010). Genetic improvement in NTUE has the potential to make an important contribution to overcoming the challenges of climate change, improving productivity and moderating the adverse effects of climate change on the sustainability of agricultural systems. It may be especially important in developing countries where poverty and lack of infrastructure limit the options of farmers to respond to climate change and who, as a consequence, are the most vulnerable to climate change.

In this chapter, the role of breeding for improved NTUE as one response to climate change will be examined. The review will focus on genetic improvement to overcome nutrient deficiencies and to enhance NTUE, yield, and grain quality. Some consideration will be given to the effects of climate change on nutrient supply from the soil and nutrient demand by crops as this will influence the nutrient balance of cropping systems and NTUE. The focus of the chapter will be on nitrogen (N) and phosphorus (P) nutrition and improvements in the efficient use of these nutrients.

10.2 Current Patterns of Nutrient Use and Nutrient Use Efficiency

The past 50 years has witnessed a large increase in the use of fertilizer, which has occurred at a faster rate than grain production (Hinsinger et al. 2011). While global consumption of N and P fertilizer has increased, average rates of nutrient application and trends in fertilizer consumption vary considerably between regions (Fig. 10.1). The largest and most consistent increases in fertilizer consumption have occurred in Asia, while Africa has shown only modest increases in the rate of N fertilizer and a decline in the rates of P application since the 1980s. Average application rates of N and P in Africa are the lowest of all the regions. Fertilizer rates in Europe and the Americas increased until the 1990s after which time rates either stabilized (in the Americas) or declined (Europe) as a nutrient replacement strategy was developed and stringent nutrient management policies were introduced (Vitousek et al. 2009; Ott and Rechberger 2012). Globally, the increases in the rates of N application have generally occurred at a faster rate than P and consequently the N: P balance of applied fertilizer has widened. The consequence of this shift in fertilizer nutrient balance to adaptation to climate change is not known, although responses to N and to elevated CO_2 can be limited if P nutrition is suboptimal (Conroy 1992; Edwards et al. 2005; Gentile et al. 2012).

The effects of these trends in fertilizer consumption on fertilizer use efficiency are illustrated in Fig. 10.2. The apparent fertilizer use efficiency has generally declined in Asia, Europe, and the Americas as the rates of application increased, whereas in Africa, the substantial increases in N and P use efficiency since the 1980s reflect the low rates used and, with P use efficiency (PUE), the decline in P application over recent times. Rather than indicating efficient use of nutrients, the high fertilizer use efficiency in Africa is symptomatic of the gradual impoverishment of the soil (Edmonds et al. 2009). Europe has also seen an increase in P efficiency corresponding to the reduction in P application rates.

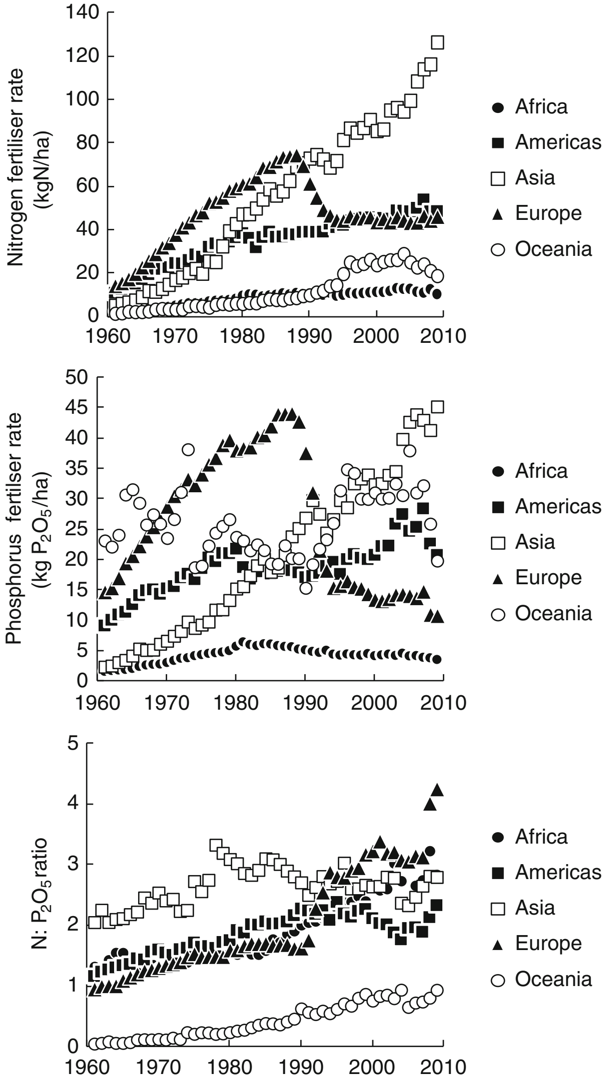


Fig. 10.1 Changes in the nitrogen (N) and phosphorus (P_2O_5) fertilizer application rates and the ratio of N:P_2O_5 applied between 1960 and 2010. Fertilizer rates were estimated from the total amount of fertilizer consumed in each year and the total area of arable land and permanent crops (*Source*: FAOStat accessed April 2012)

The changes in fertilizer use over the last 50 years have resulted in marked regional differences in soil fertility that have important implications for future efforts to improve NTUE. The level of soil fertility can influence the physiological basis of NTUE, which will influence breeding objectives and selection criteria. When soil nutrient availability is low, traits associated with acquisition and uptake

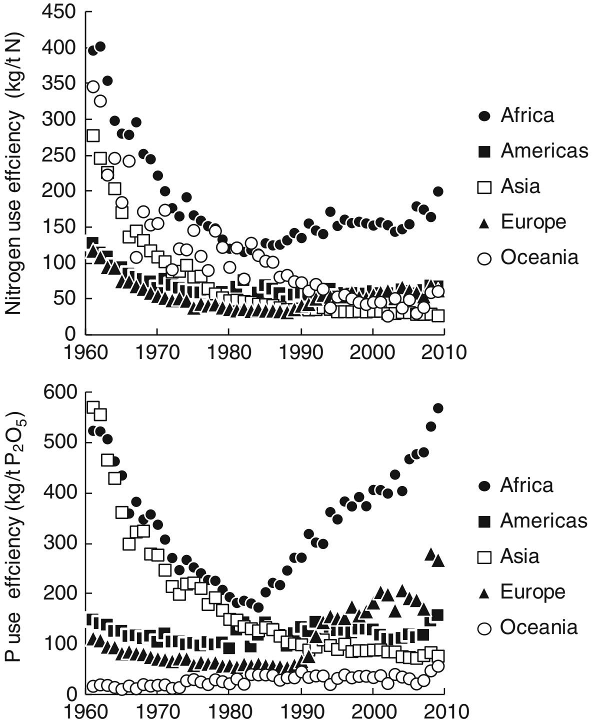


Fig. 10.2 Estimates of the N and P use efficiency between 1960 and 2010. The fertilizer use efficiency was based on the total production of cereals, coarse grains, pulses, oilseeds, fiber crops, and tuber and root crops in each year and the total N and P_2O_5 consumed in each year (*Source*: FAOstat accessed April 2012)

of nutrients tend to be important, while at high levels of fertility, when nutrient availability is less limiting to yield, traits related to utilization of the nutrient may become relatively more important (Ortiz-Monasterio et al. 1997; Wang et al. 2010).

In parts of Western Europe, China, and the USA, N and P are applied in excess of the crops' requirements, and this overfertilization has resulted in low NTUE and loss of nutrients from the agricultural system. As a result, degradation of soil and water systems is an issue in these regions (Khan et al. 2007; Vitousek et al. 2009; Wenqi et al. 2009; Wenqi et al. 2011; Ott and Rechberger 2012). In Australia, where soils over much of the agricultural areas are naturally low in P, farm gate P balances are positive with a high proportion of soil tests showing values well above the critical value (Weaver and Wong 2011). Detailed nutrient budgets for N and P illustrate the low recovery and poor efficiency of nutrient use. In China, only 4–13 % of the N fertilizer and 1–3 % of the P fertilizer applied to agricultural land are recovered in food (Wenqi et al. 2009, 2011). In the European Union, it has been estimated that net per capita consumption of P by agriculture is 4.7 kg P per year of which only 1.2 kg P per year is recovered in food (Ott and Rechberger 2012). In this instance, the P is estimated to be accumulating in agricultural soil at a rate of 2.9 kg P/ha per year. Breeding programs to improve NTUE in these regions will be conducted against a background of high levels of soil fertility and static or falling inputs of fertilizer.

In stark contrast, crops over large areas of sub-Saharan Africa receive suboptimal applications of fertilizer and suffer from chronic nutrient stress. This has limited productivity and has led to nutrient mining of soil and a drawing down of the soils' nutrient reserves (Edmonds et al. 2009; Vitousek et al. 2009). Improving NTUE therefore needs to be conducted in parallel with efforts to increase the soil nutrient base by the use of increased rates of fertilizer and inputs of organic matter and N.

10.3 Nutrient Use Efficiency

10.3.1 Definitions of Nutrient Use Efficiency and Implications for Breeding

NTUE is a deceptively simple term, which is used inconsistently (Table 10.1). There is a variety of terms used to describe how plants respond to nutrient supply. In some cases, the same measure of efficiency is called by different names and in others the same term is defined in different ways. Agronomic efficiency, in which the emphasis is placed on recovery of and response to fertilizer by a crop, may not be appropriate for genetic efficiency, where it may be better to exploit native soil reserves more effectively to reduce reliance of mineral fertilizer. There is little consensus on which definition is the most appropriate in breeding for improved nutrient efficiency.

Breeding for improved NTUE will be influenced in part by how NTUE is defined because it will affect the screening method used, including the measurements that need to be taken, whether fertilizer treatments need to be imposed and the selection of sites for assessment. More importantly, the type of germplasm that is developed can differ depending on which definition of NTUE is used to guide selection. The problem associated with the definition of NTUE in breeding for improved nutrient efficiency has been recognized for some time (Blair 1993; Gourley et al. 1994) but is far from being resolved.

One commonly used definition is that proposed by Moll et al. (1982), which was originally used for N use efficiency (NUE) but which has been subsequently extended to other nutrients (Ortiz-Monasterio et al. 2001). It is defined as the yield per unit of nutrient supplied (Table 10.1) and it has two components: the ability to extract nutrients from the soil (uptake efficiency) and the ability to convert the nutrients absorbed by the crop into grain (utilization or physiological efficiency). While plants derive their nutrients from soil and fertilizer, nutrient supply is often considered to be the nutrients supplied as fertilizer and thus NTUE is often the yield per unit of fertilizer applied. A problem with using this definition to identify more efficient genotypes is that one is essentially selecting for yield potential. If it is used to assess NTUE of a diverse range of genetic material, lower yielding varieties (such as landraces or old varieties) will have low NTUE

Table 10.1 Some terms used to assess efficiency in nitrogen and phosphorus studies

Efficiency term	Description	References
Nutrient use efficiency (I)	Shoot biomass per unit nutrient supplied	Steenbjerg and Jakobsen (1963)
Nutrient use efficiency (II)	Shoot biomass per unit nutrient uptake	Wissuwa et al. (1998)
Shoot nutrient utilization efficiency	Shoot biomass per unit nutrient uptake	Su et al. (2006)
Biomass utilization efficiency	Biomass yield per unit nutrient uptake	Su et al. (2009)
Nutrient use efficiency (grain)	Grain yield per unit nutrient supplied	Moll et al. (1982), Manske et al. (2002)
Nutrient uptake efficiency (I)	Total nutrient uptake per unit nutrient supplied	Moll et al. (1982), Osborne and Rengel (2002)
Nutrient uptake efficiency (II)	Total nutrient accumulated per unit root weight or length	Liao et al. (2008)
Nutrient acquisition efficiency	Total nutrient uptake per unit nutrient applied	Osborne and Rengel (2002)
Nutrient efficiency ratio (I)	Grain yield per unit nutrient uptake	Jones et al. (1989)
Nutrient efficiency ratio (II)	Shoot growth at low nutrient relative to shoot growth at high nutrient	Ozturk et al. (2005)
Nutrient utilization efficiency	Grain yield per unit nutrient uptake	Moll et al. (1982), Manske et al. (2002)
Shoot nutrient utilization efficiency	Shoot biomass per unit P uptake (shoots and roots minus seed P reserve)	Osborne and Rengel (2002)
Relative grain yield	Grain yield at low nutrient supply relative to grain yield at high nutrient supply	Graham (1984)
Apparent recovery	Net uptake of nutrient per unit nutrient applied	Crasswell and Godwin (1984)
Agronomic efficiency	Net increase in grain yield per unit nutrient applied	Crasswell and Godwin (1984), Hammond et al. (2009)
Physiological efficiency	Net increase in grain yield per unit net increase in nutrient uptake	Crasswell and Godwin (1984)

even if they possess traits that may enhance nutrient uptake and use. Clearly, differences in yield potential confound assessment of efficiency when this definition is used.

Another definition, which is used frequently, is based on the relative yield at low and adequate levels of nutrient supply. Graham (1984) defined nutrient efficiency as the ability of a variety to produce a high yield in soil that is limiting in the particular nutrient. Consequently an efficient variety is one that has a high relative yield. Nutrient efficiency is estimated by growing plants at two rates of nutrient supply and calculating the ratio of biomass or yield at low (or zero) and high rates of

Table 10.2 Nitrogen use efficiency of a range of maize genotypes when classified using different definitions of efficiency

	Grain yield		NUE			
Hybrid	Low N g per plant	High N	Low N (g/gN)	High N	Agronomic eff. (g/gN)	Relative yield (%)
1	223	243	90.3	24.6	2.7	91.8
2	218	275	88.3	27.8	**7.7**	79.3
3	185	217	74.9	21.9	4.3	85.3
4	270	310	109.3	31.3	5.4	87.1
5	180	195	72.9	19.7	2.0	92.3
6	264	319	106.9	**32.3**	7.4	82.8
7	297	276	**120.2**	27.9	-2.8	**107.6**
8	254	257	102.8	26.0	0.4	98.8

The hybrids were grown at low (2.47 gN per plant) and high (9.88 gN per plant). The most efficient hybrid is highlighted in bold for each definition. NUE is the grain yield divided by the N supply, agronomic efficiency is the increase in yield per unit of additional N, and relative yield is the yield at low N divided by the yield at high N (Adapted from Moll et al. 1982)

fertilizer. However, differences in yield potential can again affect the interpretation of results. Variation in biomass and yield is generally less under nutrient stress than under a nonlimiting supply of nutrients when differences in yield potential are expressed more strongly. Consequently a variety with a low yield potential may show a higher nutrient efficiency compared to a variety with a high yield potential (Gourley et al. 1994).

The problem of yield potential confounding interpretation of nutrient efficiency can be addressed by considering the two aspects separately. The responsiveness of a variety and its yield potential can be viewed as separate traits, and so varieties can be classified into four groups: low yielding and responsive, low yielding and nonresponsive, high yielding and responsive, and high yielding and nonresponsive (Blair 1993). This approach is useful when genotypes that differ widely in the yield potential are examined.

Different definitions of NTUE target different aspects of nutrient uptake and utilization, which creates the dilemma that genotypes may vary in their efficiency rankings depending on the definition used (Blair 1993; Gourley et al. 1994). The problem is illustrated using data from Moll et al. (1982) in Table 10.2, in which the ranking of the maize hybrids changes according to the criterion used to identify NTUE. The most appropriate criterion will most likely depend on the environment and the farming system that is being targeted.

10.3.2 Crop Responses to Nutrients and Nutrient Use Efficiency

Crops show a diminishing response to increasing supplies of a nutrient (Fig. 10.3a), which is most commonly described by the Mitscherlich curve. The *Y*-intercept represents the ability of crops to utilize native soil nutrients and the slope of the curve represents the responsiveness to each increment of additional nutrient and is related to the efficiency of nutrient use. Efficiency is greatest at the lowest rates of fertilizer use when the crops are most responsive and diminishes as the fertilizer rates approach that required for maximum yields.

Genetic improvement in NTUE can increase the ability to use native soil nutrients without altering the yield potential of the crop (Variety B), which will reduce the amount of fertilizer required to reach maximum yield. Increasing the yield potential alone (Variety C) may not alter the amount of fertilizer required to reach maximum yield but will increase the yield achieved for a given rate of a fertilizer below the optimum rate and thus may improve the profitability of fertilizer use. Increasing both the ability to exploit the native soil nutrients as well as increase the yield potential (Variety D) will enable lower fertilizer rates to be used as well as provide higher yield for a given rate below the optimum.

These differences in the ability to acquire nutrients and in yield potential highlight the problems of defining NTUE (Fig. 10.3b–d). Using the definition of Moll et al. (1982), sees relatively little variation in NTUE and the NTUE of the four genotypes quickly converge, reflecting the trends in grain yield (Fig. 10.3b). This is hardly surprising given this definition of NTUE means that efficiency is inversely related to nutrient supply. Using relative grain yield as the definition of NTUE sees a greater separation between varieties based on their ability to utilize native soil nutrients (Fig. 10.3c). If there are significant differences in grain yield at low levels of nutrient availability, differences in relative yield should be able to separate varieties. Agronomic efficiency (Fig. 10.3d) is also influenced by a variety's ability to exploit native soil nutrients; however, the important difference to note is that varieties with a high relative grain yield ("efficient" varieties) have a low agronomic efficiency, and thus, selection for genotypes with high relative yield may lead to varieties with low agronomic efficiency. The other point to note is that all measures of nutrient efficiency decline as fertilizer rates increase and genetic differences tend to be greater at lower levels of nutrient supply.

10.3.3 Breeding for Nutrient Use Efficiency

The case for breeding for greater nutrient efficiency has been argued strongly in the past (Graham 1984; Graham et al. 1992; Graham and Rengel 1993; Rengel 1999; Fageria et al. 2008; Khoshgoftarmanesh et al. 2011). If breeding for improved NTUE is to be successful, a number of conditions need to be met: (a) there needs to be useful genetic variation in NTUE; (b) the genetic basis of the trait needs to be understood; and (c) appropriate selection criteria need to be defined, which often will require an understanding of the important physiological determinants of nutrient efficiency. There also needs to be no yield penalty associated with improvements in nutrient efficiency.

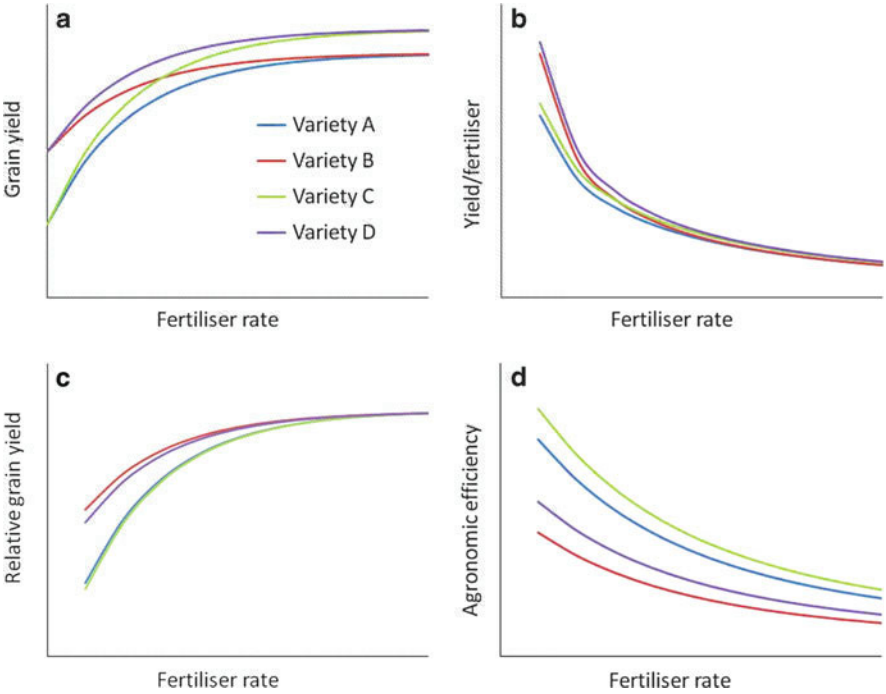


Fig. 10.3 Possible effects of genetic differences in nutrient acquisition and response to fertilizer on different measures of nutrient use efficiency. Variety A is the standard variety. Variety B has the same yield potential but is able to extract soil nutrients more effectively than Variety A. Variety C has a higher yield potential than Variety A, while Variety D has both a higher yield potential and an improved ability to exploit soil nutrients. The graphs show (**a**) the grain yield response to fertilizer inputs and the differences in nutrient use efficiency when defined as (**b**) yield divided by fertilizer applied (Y/F; Moll et al. 1982), (**c**) relative grain yield (Y_f/Y_{max}; Graham 1984), or (**d**) agronomic efficiency ($(Y_f\text{-}Y_0)/F$). Y_0 is the grain yield with no fertilizer, Y_f is the grain yield at a given fertilizer rate, Y_{max} is the grain yield at a nonlimiting rate of fertilizer, and F is the fertilizer rate

10.3.3.1 Genetic Variation in Nutrient Use Efficiency

Over the past 30 years, there has been a considerable amount of work that has characterized genetic variation in nutrient efficiency among the major food crops (Graham and Nambiar 1981; Graham 1984; Marcar and Graham 1987; Graham and Rengel 1993; Grewal et al. 1997; Ortiz-Monasterio et al. 1997; Cianzio 1999; Rengel 1999; Stangoulis et al. 2000; Baligar et al. 2001; Fageria et al. 2002; Torun et al. 2002; Hacisalihoglu et al. 2004; Yan et al. 2006; Hirel et al. 2007; Genc and McDonald 2008; Rengel and Damon 2008; Balint and Rengel 2009). This has demonstrated that there are significant levels of genetic variation in nutrient efficiency among genotypes of staple food crops, which can be exploited in breeding programs. Despite this, progress in developing nutrient efficient crop

Table 10.3 Examples of the release of nutrient use efficient varieties or of germplasm development programs targeted specifically for improved nutrient use efficiency

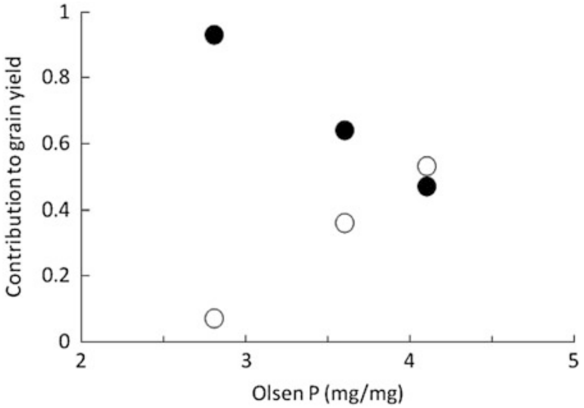
Nutrient	Crop	Region	Reference
Nitrogen	Maize	Southern and eastern Africa	Bänziger et al. (2006)
	Sugar cane	Brazil	Baldani et al. (2002)
Phosphorus	Soybean	China	Yan et al. (2006)
	Rice		Chin et al. (2011)
	Wheat	China	Yan et al. (2006)
	Common bean	Central America	Lynch (2011)
		Mozambique	McClean et al. (2011)
Manganese	Barley	South Australia	Jennings (2004), McDonald et al. (2001)
Iron	Soybean	USA	Wiersma (2010), Rodriguez de Cianzio (1991)
	Oat Sorghum Common bean	USA	Rodriguez de Cianzio (1991)
	Chickpea	WANA	Saxena et al. (1990)

varieties has been slow (Fageria et al. 2008; Wissuwa et al. 2009), and there are few varieties that have been released specifically for improved NTUE (Table 10.3). Apart from conventional breeding methods, a transgenic approach has recently been used to develop lines of canola and rice requiring lower inputs of N fertilizer (Good et al. 2007; Shrawat et al. 2008). The slow progress is due to many factors: nutrient efficiency is a complex trait subject to considerable environmental variation, appropriate screening methods have been slow to be developed because of a poor understanding of the most limiting physiological processes, and the genetic control of nutrient efficiency is not well understood. At a pragmatic level, it is likely that many commercial plant-breeding programs in developed countries have viewed improved NTUE as peripheral to their major breeding objectives compared to characters such as disease resistance, quality, drought tolerance, and yield per se.

10.3.3.2 Mechanisms of Nutrient Use Efficiency

Several reviews have described the mechanisms of efficiency for a number of nutrients (Cianzio 1999; Rengel 1999; Cakmak and Braun 2001; Fageria et al. 2008; Khoshgoftarmanesh et al. 2011). The strategies used by plants to promote uptake and enhance yield can be considered in terms of two fundamental processes (a) the ability to acquire nutrients from the soil and (b) efficiency with which nutrients taken up by plants are used to produce biomass and grain. Mechanisms of nutrient acquisition include alterations to the chemical and biological properties of the rhizosphere to increase nutrient availability, increases in the volume of soil

Fig. 10.4 The contributions to grain yield of phosphorus uptake efficiency (*filled circle*) and phosphorus utilization efficiency (*open circle*) among genotypes of bread wheat grown on a phosphorus deficient acid soil over 3 years (From Manske et al. 2001)



explored by increased root growth and changed root architecture, interactions with microbial populations in the rhizosphere, and changes in the expression of ion transporters in the roots to enhance uptake. Efficiency of utilization may include greater root to shoot translocation of nutrients, compartmentation of nutrients and partitioning within the plant, metabolic efficiencies and greater remobilization. The relative importance of different mechanisms is likely to vary with the severity of nutrient stress. Under severe deficiency, the ability to take up nutrients may be critical to meet the demands of the crop, particularly for nutrients that have low mobility (e.g., P) or which are present in very low concentrations, such as the micronutrients. When the concentration of available nutrients in the soil is high and uptake is less of a limitation, utilization efficiency may become more important to nutrient efficiency (Manske et al. 2002; Hirel et al. 2007; Wang et al. 2010; Rose and Wissuwa 2012). Figure 10.4 illustrates this effect in a study on the genetic variation in PUE: the importance of uptake efficiency is equal to or greater than that of utilization efficiency in each year, but its importance increases as the severity of the deficiency increases. There is some evidence to suggest that modern cultivars of crop plants developed for high input and intensive systems have lost the capacity to acquire some soil nutrients when availability is low (Wissuwa et al. 2009), which likely reflects the change in efficiency mechanisms as soil nutrient availability increases (Fig. 10.4).

While there can be some debate whether selection for nutrient efficiency should be based on traits associated with uptake or utilization efficiency (e.g., Wang et al. 2010; Rose and Wissuwa 2012), the natural variation in nutrient availability across sites and seasons may mean that both uptake and utilization will contribute to nutrient efficiency and their relative importance will vary with the availability of soil nutrients. If breeding for nutrient efficiency is targeting a region where soil nutrient availability is variable, both uptake efficiency and utilization efficiency are useful and should be combined.

10.4 Predicted Impacts of Climate Change and Implications for Nutrient Use Efficiency

The predicted effects on climate of changes in atmospheric concentrations of greenhouse gases and the consequences for local agricultural production are variable, with marked differences between regions (IPCC 2007; Jarvis et al. 2010; Olesen et al. 2011). Analysis of recent trends in rainfall between 1900 and 2005, for example, has shown that the eastern parts of North and South America, northern Europe, and north and central Asia have experienced increased rainfall, while the Sahel, the Mediterranean Basin, South Africa, and parts of south Asia have shown a drying trend (IPCC 2007). Despite the high degree of variability in regional and temporal trends, there is consistency in a number of long-term observations, which is concerning for agricultural production in the future. It is predicted that the world will face a generally warming climate with a greater frequency of warm spells and heat stress. Precipitation will be more variable and there will be a greater frequency of heavy precipitation and of drought, even in regions where annual precipitation is predicted to increase. For many regions of the world, nutrient management needs to be done in an environment of elevated CO_2, increased rates of N deposition, increasing temperatures, and more variable precipitation with a higher frequency of drought.

It is difficult to predict the consequences of these changes to nutrient use and NTUE because there are potential effects on soil properties and soil biological activity, on the growth of plants and their ability to take up nutrients, and on the partitioning of nutrients within the plant. Our understanding of the influence of many of the effects is poor, especially when they change together. Many past studies have been conducted in single factor experiments and have speculated on changes into the future without regard to the interactions that may occur. For example, rising atmospheric CO_2 levels can enhance plant biomass production (Long et al. 2004; Mittler and Blumwald 2010) and thus increase the demand for many nutrients, but the increase in temperatures that will accompany increases in CO_2 will hasten development, shorten the length of the growing season, and may reduce the demand for and uptake of nutrients (Nord and Lynch 2009). Other effects of individual components of climate change may influence nutrient uptake in different ways. Higher temperatures may increase transpiration rates by increasing atmospheric vapor pressure deficit, which may increase water flow to the roots and increase transport of some nutrients by mass flow, but may also lead to more rapid soil drying, which can reduce nutrient uptake.

Much of the past work on the effects of climate change on crop nutrition has focused on N nutrition (Lynch and St. Clair 2004). This is not surprising given the importance of N to crop growth and yield and the large quantities of N applied to crops (Fig. 10.1). However it tends to distort our understanding of the impact of climate change and underestimates the importance of nutrient balance in plants to productivity and NTUE.

Another aspect that is sometimes overlooked in discussions on plant responses to changing climate is the plasticity in growth and development that plants possess and, in the long term, the ability to respond to and adapt to changes in climate. Root systems respond to local variation in moisture and nutrients in the soil and are effective in integrating nutrient uptake in a heterogeneous soil environment. Long-term adaptation may also have profound influences on how plant nutrient demand changes in the future. For example, a community of spruce trees that had been growing under elevated levels of CO_2 for over 100 years because of their proximity to springs that emitted CO_2 had a lower rate of photosynthesis than nearby tress that had grown under normal CO_2 levels (Cook et al. 1998). The lower photosynthesis rate was associated with lower concentrations of chlorophyll in the leaves and a higher photosynthetic efficiency. It has been suggested that if this was a common response in other species, the greater photosynthetic efficiency would lead to a lower demand for nutrients involved in photosynthesis—N, sulfur (S), magnesium (Mg), and iron (Fe) (Brouder and Volenec 2008).

In its simplest terms, the nutrient status of a crop reflects the balance between the ability of the soil to provide nutrients to the crop and of the root system to take up nutrients (supply) and the nutrient required by the crop for optimum growth (demand). The two processes are not independent and there will be feedback between plant growth and aspects of soil nutrient availability. A study by Patil et al. (2010) illustrates this. Climate change is predicted to cause increases in rainfall and soil temperature in some regions of the world. In a lysimeter study, higher rainfall increased nitrate leaching during winter potentially reducing supply of N, but this was counteracted by warmer soils increasing crop growth rates, which increased demand and N uptake. Notwithstanding soil–plant interactions such as this, the net effect of climate change on crop nutrition will be a consequence of its relative effects on nutrient supply and demand. The success of genetic improvement to respond to changes in climate will depend on whether changes in availability and supply of nutrients or changes in the ability to acquire nutrients by changes in root growth and physiological efficiency will be more influential in meeting changes in plant demand for nutrients.

10.4.1 Soil Properties, Nutrient Availability, and Supply to the Roots

At present the impact of climate change on soil properties and its subsequent effect on mineral nutrient supply is largely conjectural because of the complexity of the soil system and the lack of long-term empirical data from agricultural systems. There are a number of ways that changes in climate can affect the availability of soil nutrients and their movement to the roots (Table 10.4). While the effects of these

Table 10.4 Possible effects of changes in climate on availability of nutrient in soil (Adapted from St. Clair and Lynch 2010)

Process	Influential climate change variables	Mineral nutrients affected
Transpiration-driven mass flow	CO_2, temperature, rainfall, vapor pressure deficit	Nitrate, sulfate, calcium, magnesium, silicon
Diffusion	Rainfall, temperature	Phosphorus, potassium zinc, iron
Soil C content and C cycling	CO_2, temperature, rainfall	Many nutrients
Leaching	Rainfall	Nitrate, sulfate, calcium, magnesium
Arbuscular mycorrhizae	CO_2, soil moisture	Phosphorus, zinc
Soil erosion	Rainfall	All nutrients
Soil pH	Rainfall, CO_2	Aluminum, manganese, copper, manganese, zinc, iron

individual factors have been the subject of much research, it is still unclear how they will interact to determine the effects of climate change on nutrient availability and how it will influence NTUE. When reviewing the influence of climate change on soil N cycling, Bijay-Singh (2011) observed:

> *. . . effects of climate change on soil N transformations can be complex, and the long-term implications on N retention and N use efficiency are unclear.*

This statement summarizes our current state of understanding of the influence of climate change on the availability of soil N, a nutrient that has been the subject of intense research over many years: our understanding of the effects of climate change on the availability of other nutrients is even less. In part this is because the drivers of climate change can affect a number of different soil processes, and sometimes in different ways; however in much of the previous research into the effects of climate change, the response to one factor is often viewed in isolation from other climatic factors that may change at the same time. For example, rising atmospheric CO_2 levels induces stomatal closure and can reduce transpiration (Long et al. 2004), which has been suggested to reduce nutrient movement to roots by mass flow (St. Clair and Lynch 2010). However mean temperatures will also rise with increases in atmospheric CO_2, which will tend to increase transpiration by increasing atmospheric vapor pressure deficits. The very complexity of the soil–plant interaction in determining nutrient uptake and plant nutrient status requires multifactor experiments be conducted and that field data from long-term CO_2 enrichment experiments be collected. Alternatively, modeling approaches can be used to study the effects of climate variability on soil–plant–atmosphere interactions and investigate the impacts of climate change on nutrient cycling, plant growth, and nutrient uptake. Combining genetic and genomic information with crop simulation modeling can potentially provide a powerful tool for future studies on the influence of climate change on crop production.

10.4.1.1 Effects of Elevated CO_2

Soil organic matter has a central role in determining soil nutrient availability. Consequently, the potential influence of climate change on nutrient availability in the soil will be influenced by the changes in organic matter and the rates of organic matter cycling. Carbon and N are linked in the soil organic matter and changes in carbon cycling will also be reflected in changes in N cycling (Bijay-Singh 2011). Recent reviews strongly suggest that climate change will affect carbon and N cycling in soils (Bijay-Singh 2011), which in turn can alter other soil properties such as pH (Rengel 2011) that can also determine soil nutrient availability.

In one of the few long-term studies of the effects of CO_2 enrichment, it was found that soil under a pasture from an 11.5-year free air CO_2 enrichment experiment had lower available P (Olsen P 18 μg/L cf 25 μg/L) but similar available N (7.61 mg/kg cf 7.86 mg/kg) compared to pasture grown under ambient CO_2 (Gentile et al. 2012). This was associated with lower concentrations and content of P in the leaves of ryegrass and a lower response to N fertilizer. The lower available P was attributed to increased sequestration of P in the soil organic matter. Reductions in the availability of P associated with elevated CO_2 have also been reported in heathland soils (Andreson et al. 2010). If a long-term effect of elevated CO_2 is to reduce soil available P, the requirements for P fertilizer may increase and the need for more P efficient genotypes and farming systems will become greater.

10.4.1.2 Temperature

The predicted increases in atmospheric temperatures are likely to increase mean soil temperatures and there is evidence that some soils have warmed during the twentieth century (Qian et al. 2011). Increased soil temperature can increase nutrient uptake by plants (Singh and Subramaniam 1997; Bassirirad 2000), which is associated with changes in soil nutrient availability as well as changes in root growth.

Temperature is a major influence of organic matter turnover (Sanderman et al. 2010; Baldock et al. 2012), although its effect on decomposition of soil organic carbon will be influenced by other environmental factors that control the soil's biological activity and which determine the accessibility of soil organic carbon to degradative enzymes (Baldock et al. 2012). Modeling has suggested that global soil organic matter levels will decline as temperature increases, although local responses may vary (Jones et al. 2005), and there is considerable uncertainty about the temperature sensitivity of soil organic matter decomposition (Davidson and Janssens 2006). However, accelerated loss of soil organic matter will reduce available soil nutrients and increase the risk of nutrient stress over the long term unless inputs of organic carbon in farming systems can increase. Greater inputs of N fertilizer to boost crop production may not be successful in halting the decline (Khan et al. 2007).

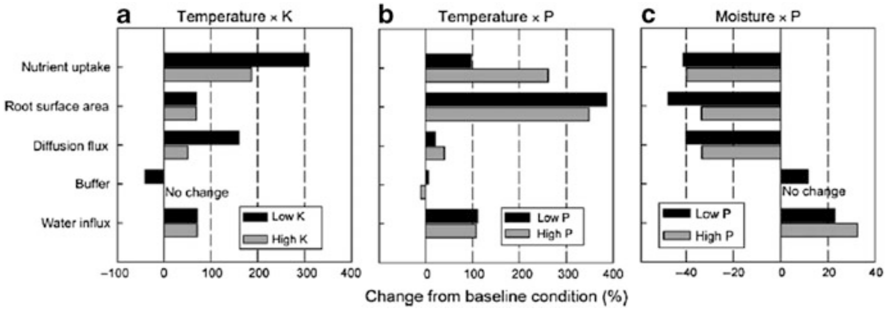


Fig. 10.5 The effect of temperature or moisture on nutrient uptake by maize roots and on parameters of soil nutrient availability and root growth. The responses are shown as the percentage change from the baseline or control conditions and are based on experiments where (**a**) root zone temperature was increased from 15 °C to 29 °C at two rates of potassium, (**b**) root zone temperature was increased from 18 °C to 25 °C in low and high P-fertility soils, and (**c**) the root zone moisture potential was reduced from −33 kPa to −170 kPa in soils differing in P fertility (Brouder and Volenec 2008) (with permission)

Mineralization rates are higher in warmer soils (Bijay-Singh 2011; Lal 2011), and rates of nutrient adsorption and desorption may change (Barrow and Shaw 1975), which will alter nutrient availability. As well, warmer soils may increase rates of diffusion and water uptake (Fig. 10.5a, b) thereby increasing nutrient delivery to the roots, although any benefits of these responses to soil temperature will clearly depend on soil moisture (Brouder and Volenec 2008; St. Clair and Lynch 2010). Therefore, if there are no major limitations to nutrient uptake, such as intermittent drought, nutrient uptake by plants may be enhanced and this may help overcome some of the nutrient dilution effects often reported in plants grown at elevated CO_2. However, caution needs to be exercised when making generalized statements about the effects of temperature on soil nutrient availability and especially if extrapolating from short-term experiments. Bassirirad (2000) highlights the fact that the effect of temperature may not be similar over all temperature ranges and that there is evidence of differences among species in their sensitivity to rising soil temperatures. Short-term improvements in nutrient delivery from greater rates of mineralization may not be sustainable in the longer term if soil organic matter declines.

10.4.1.3 Water Availability

Changes in climate will see local variation in the distribution and intensity of rainfall. In many regions, more frequent periods of dry weather are predicted, and this may reduce nutrient availability and movement to the roots due to lower rates of mass flow and diffusion (Dunham and Nye 1976; Mengel and Kirkby 2001). However, Brouder and Volenec (2008) suggest the influence of changes in mass flow for immobile soil nutrients will be small because simulation modeling suggests total nutrient uptake is insensitive to changes in water flows to the root. They also argue that reducing soil moisture to the point that delivery of mobile nutrients to the roots by mass flow limits nutrient uptake would more than likely limit root and shoot growth by greater plant water deficits. Mass flow and diffusion are overlapping mechanisms of nutrient delivery to the root, and their relative importance varies with root zone conditions rather than with a specific nutrient. Consequently, there may be relatively little change in nutrient uptake as soil dries and as the balance of delivery changes from mass flow to diffusion. At some point however diffusive transport will be insufficient to meet the plants' demand and nutrient uptake will be reduced (Fig. 10.5c).

10.4.1.4 Implications for Nutrient Use Efficiency

While climate change will alter a number of soil processes that affect soil nutrient availability and potentially affect the delivery of nutrients to the roots, the consequences of these changes to nutrient availability and the subsequent influences on nutrient uptake and NTUE are unclear. It is likely that accelerated loss of soil organic matter and greater periods of dry weather as a result of climate change will reduce the availability of nutrients over the long term and increase the risk of nutrient stress developing. Reductions in supply of nutrients will require crop varieties that are better at exploiting supplies of nutrients to maintain nutrient uptake and that make more efficient use of fertilizer. While the magnitude of the effect is uncertain, any decreases in soil nutrient availability as a result of climate change will increase the need to improve crop NTUE in the face of declining high-quality nutrient reserves and increasing costs of fertilizer.

10.4.2 Growth, Yield, and Nutrient Demand

There is still some uncertainty about the consequences of climate change on crop yields (Jarvis et al. 2010). There will be large regional variation in the responses and the effects on productivity will also depend on the capacity of farmers to adapt to changes in their environment (Lobell and Burke 2010). Nevertheless, to meet the predicted demands for food in the future, increases in yield need to be sustained in the face of increased frequency of heat and drought stress, and this will require commensurate changes in nutrient uptake. The concentrations of some nutrients such as potassium and zinc (Zn) may also help plants cope with the predicted increases in abiotic and biotic stresses that will be associated with climate change (Cakmak 2000; Walters and Bingham 2007; Amtmann et al. 2008; Peck and McDonald 2010). Acquisition of nutrients, therefore, becomes an important component in the capacity of plants to adapt to the changes in growth and nutrient availability that may result from climate change.

10.4.2.1 Increases in Shoot Growth and Yield

Shoot biomass in C_3 and C_4 crop species increases under elevated CO_2 concentrations, although increases are much smaller in C_4 crop plants (Kimball et al. 2002; Long et al. 2004). Increases in yield are more variable (Long et al. 2004); however, yield increases in C_3 crops under elevated CO_2 are frequently reported (Kimball et al. 2002). The relative increases in biomass production and yield from elevated CO_2 under water stress have been found to be equal to or greater than those under well-watered conditions, which contrast to the effect of nutrient stress: the ability of crops to respond to elevated CO_2 will depend on access to and uptake of available nutrients (Poorter 1998; Kimball et al. 2002; Luo et al. 2004; Edwards et al. 2005). Nutrient dilution at elevated CO_2 has often been reported (see below) but in many cases there is still an increased uptake of nutrients suggesting the increased demand for nutrients is often not met by increased uptake. Therefore, improvements in nutrient supply and in NTUE will be important to allow crops to take advantage of any benefits to growth and yield afforded by elevated CO_2. Genetic improvement in nutrient efficiency will make a valuable contribution to this goal.

10.4.2.2 Root Growth and Function

Modeling of nutrient uptake by plants suggests that changes in root length and surface area are important determinants of the responses of plants to changes in soil nutrient supply, soil temperature, and moisture (Barber and Mackay 1985; Mackay and Barber 1985; Brouder and Volenec 2008). The effects of changes in climate on root growth, therefore, will influence how plants can respond to changes to nutrient availability.

Changes in the partitioning of growth between root and shoot will alter nutrient balances within the plant and the nutrient composition of the shoot. Brouder and Volenec (2008) concluded that there was no significant change in the root to shoot ratio under elevated CO_2 and that changes in shoot biomass would most likely drive changes in nutrient demand. In contrast, the review of Kimball et al. (2002) found that root growth generally responded more strongly to elevated CO_2 than shoot growth and their data would suggest an average increase in root to shoot ratios of about 18 % among C_3 grasses and woody perennial crops. However, the often-reported reduction in shoot nutrient concentration under elevated CO_2 would suggest that greater partitioning to root growth may not result in uptake of nutrients sufficient to meet the additional nutrient demands of the crop.

The frequency of drought will increase as a consequence of climate change and this will reduce root growth (Weir and Barraclough 1986; Asseng et al. 1998; Buljovcic and Engels 2001). The decline may be most marked in the surface layers of soil although there may be proliferation of roots in the moist subsoil (Asseng et al. 1998). Nutrient uptake from the drying parts of the soil profile will be reduced and this is likely to lower total nutrient uptake if other parts of the profile are unable to maintain the supply of nutrients (Barber and Mackay 1985; Jupp and Newman 1987; Buljovcic and Engels 2001). The ability of roots to recover from periods of dry weather and resume nutrient uptake is also important for the nutrition of crops. Rewetting of the soil profile can lead to renewed root growth and water uptake, but there may be a considerable delay in the time of recovery. Studies on P uptake by Jupp and Newman (1987) found that uptake to the shoot was low following rewatering and there was some evidence of recovery only after 2 or 3 weeks. In the field, recovery of water use after a period of water deficit occurred approximately 10 days after rewatering (Asseng et al. 1998).

Root growth is a key factor in nutrient absorption from the soil and this is not likely to diminish under a changing climate. Root traits are an important aspect of nutrient efficiency and breeding for root characteristics that will enhance nutrient uptake will contribute to greater NTUE. Much of the past work on root growth has examined traits related to root architecture, but differences in recovery of root growth after rewetting may also be useful traits to examine.

10.4.2.3 Phenology and Nutrient Use Efficiency

The rate of crop development influences the duration of crop growth, biomass production, and partitioning, all of which influence nutrient uptake and demand. Phenology is sensitive to temperature and an important consequence of rising global temperatures is to hasten crop development in many regions (Sadras and Monzon 2006; Grab and Craparo 2011; Webb et al. 2012), while there has been a lengthening of the growing season in high latitudes associated with an earlier onset of the growing season (Jarvis et al. 2010; Olesen et al. 2011). There is some evidence that altering plant phenology may influence nutrient acquisition (Nord and Lynch 2009). Hastened development restricts P uptake; genotypes that flower quickly and have a short vegetative phase have low biomass production and P uptake. The delay in development that is characteristic of P deficiency is considered to be an adaptation to low P as it allows a longer period of P uptake (Nord and Lynch 2008). Increased global temperatures may hasten development and reduce uptake of P, leading to a reduction in PUE. However, this prediction overlooks the effect of rising soil temperatures on P uptake. Sowing wheat early into warmer soils can result in substantial reductions in the optimum rate of P, which is most likely to be due to the effects of soil temperature on root growth and P availability in the soil (Barrow and Shaw 1975; Batten et al. 1993, 1999).

10.4.2.4 Nutrient Toxicities and Nutrient Use Efficiency

Production over large areas of the world's agricultural land is affected by a number of soil toxicities such as aluminum toxicity, salinity, and boron toxicity, which restrict root growth and limit grain yield (Lynch and St. Clair 2004; Rengasamy

2006; Yau and Ryan 2008). These chemical constraints to root growth can exacerbate the effects of drought and heat stress by reducing the ability of crops to exploit soil moisture reserves, making crops more vulnerable to reductions in rainfall and increases in temperature induced by climate change. By restricting root growth and water use, soil toxicities not only reduce grain yield but may also reduce nutrient efficiency. Apart from influencing how crops may cope with an increasingly variable climate, soil constraints such as acidity and alkalinity can have a direct effect on nutrient uptake. For example, P deficiency occurs frequently in acid soils where aluminum toxicity occurs. Breeding to alleviate the effects of soil toxicities can enhance crop nutrient efficiency indirectly (Wissuwa et al. 2009).

10.4.3 Nutrient Concentrations and Grain Quality

Changes in the frequency and severity of soil water deficits and the effects of warmer growing seasons can influence plant nutrient concentrations by altering the balance between nutrient supply and crop requirement. However, these effects will be variable as they will largely reflect the regional and seasonal variations in the patterns of rainfall and temperature. Nutrient concentrations in plants are also responsive to elevated CO_2. Plant growth can be enhanced at high CO_2, the magnitude of the effect depending on the other nutritional limitations (Poorter 1998), which can lead to nutrient dilution if the rate of nutrient uptake does not increase at the same rate as biomass production.

Nitrogen concentrations are consistently lower in leaves and grain of plants grown under elevated CO_2 (Conroy 1992; Wu et al. 2004; Taub et al. 2008; Wieser et al. 2008; Pleijel and Danielsson 2009; Erbs et al. 2010; Pleijel and Uddling 2012). Reductions in grain N concentrations have also been associated with reductions in the protein fractions that are important for bread-making quality. Flour from wheat grown under elevated CO_2 has up to 20 % less gliadin and 15 % less glutenin (Wieser et al. 2008).

The effects on other mineral nutrients are more variable (Duval et al. 2012). Among crop plants, elevated CO_2 has been reported to lower the concentrations of S (Fangmeier et al. 1997; Erbs et al. 2010; Duval et al. 2012), Zn, and Fe (Fangmeier et al. 1997; Wu et al. 2004) in the grain and foliar Mg and Zn (Duval et al. 2012), but there is considerable variation in the effect. Despite the lower concentrations of nutrients in leaves and grain, total nutrient uptake is often greater under elevated CO_2, suggesting that the availability and/or uptake of nutrients may not be impaired but that there is proportionately greater production of biomass. In some cases, elevated CO_2 can increase nutrient uptake more than the increase in shoot biomass leading to increased concentrations. Increases in shoot Fe concentrations have been reported in tomato (Jin et al. 2009) and grasses (Duval et al. 2012) and the concentrations of cadmium, Zn, manganese, and Mg increased in the shoots of the cadmium/zinc hyperaccumulator *Sedum alfredii* under elevated CO_2 (Li et al. 2012).

The often-reported reductions in the concentrations of grain N, S, and Zn at high CO_2 levels have important implications for the quality and nutritive value of the food. Low concentrations of Zn and Fe in cereal grains is a major cause of the poor dietary intake of these nutrients and the attendant chronic health problems (Graham et al. 2012). Concentrations of Zn and Fe are often closely linked to the concentrations of N and S (Uauy et al. 2006; Morgounov et al. 2007; Gomez-Becerra et al. 2010), which can affect processing quality in wheat by altering the composition of storage protein in the grain (Shewry et al. 1995; Peck et al. 2008). Most of the experiments, which have reported a decline in nutrient concentrations at elevated levels of CO_2, have been conducted in soils with high fertility and in which total nutrient uptake increased. The impact when available soil nutrients are low is not known but will probably depend on the response in crop biomass and yield at elevated CO_2. Irrespective of the effect, a consequence of rising CO_2 may be to counteract recent efforts to increase grain Zn and Fe concentrations by plant breeding.

10.5 Genomic Approaches to Improving Nutrient Use Efficiency

While it is acknowledged that there is a need to increase NTUE in the major crops, improvement has been slow. There are many reasons for the slow rate of progress. NTUE is a complex, quantitative trait that is influenced greatly by environmental factors. The physiological and molecular bases of the use efficiency of many nutrients are, in general, poorly understood and often only defined in broad terms.

As with NTUE, there has been relatively little progress in improving drought tolerance based on physiological and molecular approaches despite the considerable amount of resources devoted to the task. Drought tolerance shares many of the features of NTUE, and the past approaches of aiming to improve drought tolerance by focusing on a narrow array of traits have been questioned: instead a broader multidisciplinary approach that integrates genomic and transgenic approaches with physiological and phenological dissection of responses has been proposed (Fleury et al. 2010). Selection and verification of the value of traits associated with NTUE under field conditions in the target environments is also a critical, and arguably the most important, step in the process (Wissuwa et al. 2009).

10.5.1 General Concepts

Genetic improvement of NTUE needs to take a multidisciplinary approach, which will integrate a number of different technologies and methods that span laboratory and field-based studies. Critical steps will include (a) identifying useful sources of genetic variation for the trait in question to allow introgression of desirable characteristics or to develop appropriate populations for genetic analysis and marker development, (b) developing a reliable phenotyping system that is predictive of field performance, and (c) developing efficient and rapid selection methods based on phenotypic or genetic screening to identify superior lines in the breeding program. In a forward genetic approach, undertaking detailed studies of the physiological and molecular responses to nutrient stress will allow improved understanding of how plants sense and respond to nutrient stress, thereby allowing improved understanding of the roles of specific genes in NTUE.

10.5.1.1 Sources of Genetic Variation

While genetic variation in NTUE has been reported for many crops, improvements in NTUE may be sometimes limited by a narrow level of genetic variation within modern germ plasm (e.g., Wissuwa et al. 2009). Novel sources of genetic variation can be derived from landraces and wild relatives (e.g., Cakmak et al. 1999; Manske et al. 2001; Genc and McDonald 2008; Gomez-Becerra et al. 2010). In wheat, the greater level of genetic variation found in wild relatives can be exploited by developing synthetic hexaploids (Ogbonnaya et al. 2007; Kishii et al. 2008). Using a transgenic approach to introduce specific genes or to manipulate gene expression to improve NTUE is another potential way of introducing new levels of genetic variation (Wissuwa et al. 2009; Mittler and Blumwald 2010). Apart from its role in introducing new levels of genetic variation for NTUE, using genetically modified plants should be seen as necessary to provide functional validation of any genes identified from approaches such as quantitative trait loci (QTL) analysis.

10.5.1.2 Using Marker-Assisted Selection to Introgress Specific Traits

Phenotypic selection by conventional plant breeding is time consuming and often depends on environmental conditions. Marker-assisted selection (MAS) is a technique that involves the selection of plants carrying genomic regions associated with a particular trait of interest by using molecular markers (Babu et al. 2004). It can be based on populations derived from a biparental cross or on a defined genetic population comprised of unrelated genotypes (association mapping) to identify marker-trait associations. The potential advantages of MAS to breeding programs include:

- Increased efficiency of backcross breeding strategies
- Combining (pyramiding) genes for traits of interest
- Incorporating target QTL into breeding programs (Collard et al. 2005; Francia et al. 2005)

The success of MAS will depend on the location of the marker(s) with respect to the gene contributing to the quantitative trait. Markers located within the gene of interest are the most sought after but these usually require the target gene to be cloned (Francia et al. 2005). Generally, markers are not located within the target gene and tightly linked flanking markers are required to locate accurately the QTL controlling a trait of interest. Markers located closely either side of a QTL are used to minimize the chance of double recombination events between the QTL and both flanking markers (Doerge 2002).

Marker-assisted selection for quantitative traits is often unsuccessful (Langridge and Chalmers 2005; Schuster 2011) and despite the large number of QTLs that have been mapped for a range of nutritional traits, few have been used in practical plant breeding. There are a number of reasons for this (Francia et al. 2005) which include the uncertainty of the QTL position, deficiencies in QTL analysis leading to underestimation or overestimation of the number and magnitude of effects of QTL, an inability to detect a QTL-marker association in divergent backgrounds, and the possibility of losing target QTL due to recombination between the marker and QTL. There may also be difficulty in evaluating epistatic effects and evaluating QTL × environment interactions (Francia et al. 2005).

The recent application of array-based methods for SNP genotyping is a valuable resource for genetic improvement by MAS (Akhunov 2011; McClean et al. 2011). Phenotyping a large association mapping panel under field conditions will help to overcome some problems associated with more traditional biparental QTL mapping. In addition, the possibility exists for combining the association mapping approach with a candidate gene approach to identify genes that could be targeted for transgenic manipulation. The advantage of this approach is that the identified genes would have a clear impact for breeding as they would have been shown to be important under commercial growing conditions. Both association and QTL mapping are essential steps in improving the efficiency of selecting for improved NTUE by breeding programs.

10.5.1.3 Gene Expression Studies

Important genes and key pathways involved in NTUE can be identified by combining genetic analysis with gene expression profiles under different levels of nutrient stress. These studies may integrate genomic, transcriptomic, proteomic, and metabolomic methods to elucidate the mechanisms of the perception of nutrient stress and the subsequent regulation of the physiological responses. This integrated approach, when applied to nutritional stresses, has been termed nutrinomics (Yan et al. 2006).

10.5.1.4 A Need for Field Validation

Despite the significant advances in application of molecular and genomic methods in the analysis of nutrient stress in recent years, there is still a need to validate results under conditions that are representative of the field environments where the crops are grown. There are a number of examples in the past where promising results obtained under highly controlled conditions either failed to show any advantage or showed much smaller benefits in the more complex field environment (Wissuwa et al. 2009). It is now being increasingly recognized that genomic approaches to improvements in abiotic stress need to integrate laboratory and field studies in a holistic approach to breeding (Mittler and Blumwald 2010).

10.5.2 Genomic Approaches to Breeding to Improve Nitrogen Use Efficiency

10.5.2.1 General Concepts

Nitrogen is a major factor in plant growth and crop yield (Marschner 1995). The growth and development of plants are often profoundly affected by the form and abundance of the N supply because the form of N significantly alters intracellular metabolism (Andrews et al. 2004; Forde and Lea 2007). Nitrogen also serves as a signaling molecule, with glutamate in particular being closely regulated within very limited concentration ranges (Forde and Lea 2007). Restricted or inappropriate N supply or form of N alters development, including shoot to root ratio, root development, seed development, and the rate of senescence. Activities of enzymes of primary metabolism respond to N supply, but so do the enzymes of photosynthesis, secondary metabolism, and metabolic control.

Since N fertilizers are rapidly depleted from most soil types and symbiotic N_2 fixation in many legumes ceases in mid-season, all field crops have some degree of dependence on applications of nitrogenous fertilizer (Marschner 1995), which is supplied to the soils surrounding growing crops before or during the growing season. Plants tend to absorb N released by soil microbes in the rhizosphere, not directly from fertilizer. One estimate had the plant as the seventh organism to assimilate the average N molecule applied to the soil! Nitrogen supply clearly alters the microbiome of the rhizosphere (Garcia-Teijeiro et al. 2009). As one of the cheapest agricultural inputs ($US200–400 per ha) in many countries, N fertilizer is often applied in excess of crop needs. Since many crops are heavily fertilized directly or from the rotational crop residue, high NUE during high soil concentrations is the metric commonly often targeted for improvement by breeders and biotechnologists in this field (Lightfoot et al. 2001, 2007; Lightfoot 2008, 2009). Enhanced NUE by plants should enable crops to be cultivated under reduced N availability, with slow release fertilizers, under water and biotic stress conditions, or poor soil quality. Improving NUE in crops could enable practices directed toward reducing groundwater (Lee and Nielsen 1987; David et al. 1997) and coastal water contamination (Fig. 10.6; Cherfas 1990; Burkholder et al. 1992) by nitrates. The decrease in undesirable environmental effects and reduced dietary nitrate

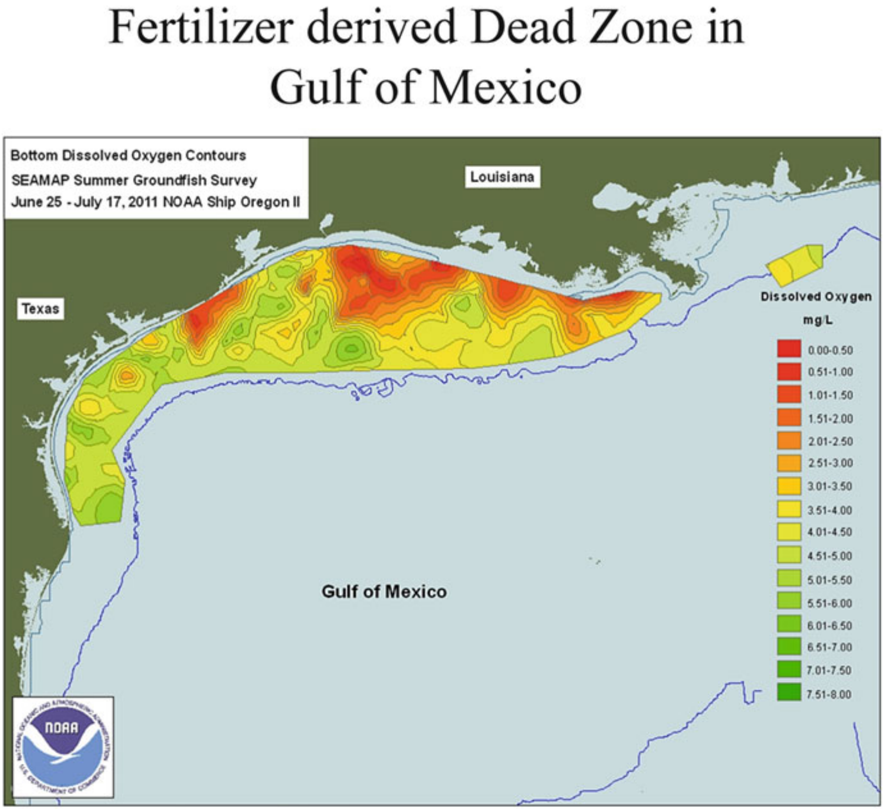


Fig. 10.6 The effect of fertilizer runoff on coastal waters (From NAOA Web site)

concentrations could decrease several human and animal health problems (Tannenbaum et al. 1978; Mirvish 1985; Moller et al. 1989).

NUE is the product of many components. At a coarse scale, NUE is an expression of:

(a) Soil supply of N
(b) N uptake efficiency
(c) Developmental influence on the size of the N sinks
(d) Remobilization and translocation within the growing plant
(e) The fraction of N translocated to the seed at harvest

Consequently on a fine genomic scale, thousands of genes and hundreds of regulatory networks contribute to NUE in plants, from seed germination to final harvest and hundreds more to the microbial activity in the soil. For brevity this section focuses on genes and regulatory networks with major effects on NUE with an emphasis on patented technologies near commercialization and pending patents.

The Two Forms of Nitrogen Use Efficiency: Regulation of Nitrogen Partitioning and Yield in Crops

Ironically, despite intensive research, the biochemical bases of the regulation of N uptake, partitioning, and tolerance to high concentrations of N are not well understood in crops or model systems (Marschner 1995; Limami et al. 1999; Specht et al. 1999; von Wiren et al. 2000; Coruzzi and Bush 2001; Seebauer et al. 2004; Terce-Laforgue et al. 2004a, b; Century et al. 2008; Coque et al. 2008; Cañas et al. 2009, 2010; Seebauer et al. 2010; Vidal et al. 2010). However, genetically and phenotypically, carbon and N partitioning and yield are clearly interrelated. NUE is one expression of this coordinated regulation. The level of available N will influence the characteristics that will contribute to NUE. Under N limitation, NUE is the ability to yield well with the available resources, while under excess fertilizer N, it is the ability to assimilate all available N. The genes underlying both forms of NUE are very different: on the one hand, assimilation will be cardinal and on the other regulation will be key. The lack of satisfactory cell-free assays and easily quantifiable substrate changes has hindered progress in understanding the molecular biology of N regulation, in contrast to N assimilation where these assays are available. However, the whole plant responses to N limitation and excess are clear and easy to score. These phenotypic changes include several characteristics that are easy to assess, such as plant size, leaf chlorosis, and early senescence, and can be used in a genetic method to isolate the important genes underlying NUE and derive an understanding on their function and biochemistry.

Microbial Activity

It has been known for many years that each molecule of fertilizer N applied to a field will be metabolized by 6–7 different microbes before it is assimilated by the target crop plant (Marschner 1995). Consequently crop plants have been bred to optimize the NUE given current fertilization practices and soil microbial compositions (Specht et al. 1999; Duvick 2005). The area of nitrification and denitrification was recently revolutionized by the identification of slow-growing Archaea as major factors (Cabello et al. 2004). Many studies of plant NUE will have to be revised in view of these unrecognized variables in experiments.

New enhanced-release fertilizers, also known as temperature-dependent slow release N fertilizers, or intelligent fertilizers, are starting to be used to increase NUE and extend N availability over a longer part of the growing season (Trenkel 1997; Garcia-Teijeiro et al. 2009). These fertilizers also change the microbial populations in soil (Fig. 10.7). Their use will provide new opportunities for the genetic improvement of crops. Methylene urea, one type of slow release N, may play a major role as an environmentally safe source of N fertilizer because of its low-leaching potential. Methylene urea has been used widely in industrialized countries at a rate of over 220,000 Mt per year. However, the NUE of plants depends on the

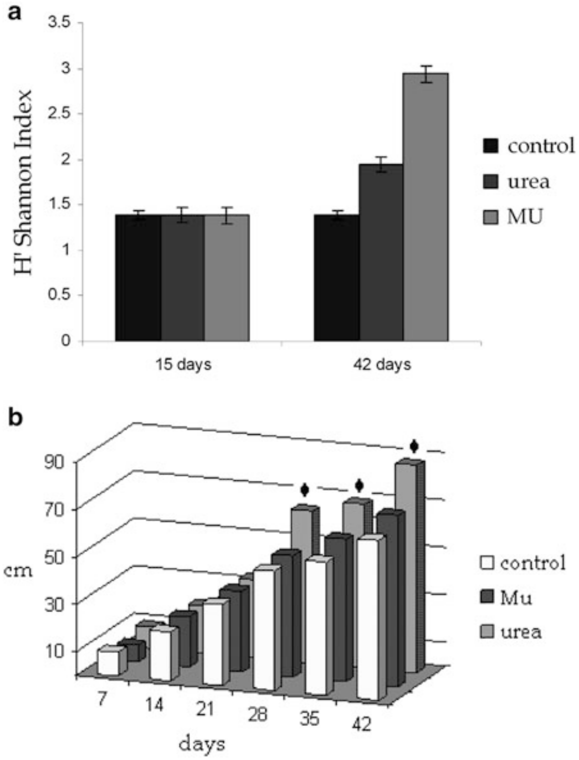


Fig. 10.7 Microbial populations are altered by N fertilization. *Panel* **a**. Shannon indexes (*H*) for characterizing soil bacterial diversity in soil treated with different N sources [urea and methylene urea (MU)] show differences develop over time. *Panel* **b**. The alterations contribute to differences in the height of corn plants (*Source*: Garcia-Teijeiro et al. 2009)

biological activity of microbes in the soil and their capacity to convert organic N into ammonium and nitrate available to the plant (Alexander and Helm 1990).

The decomposition of the methylene urea in soil is caused by both biological and abiotic factors (Koivunen and Horwath 2004; Koivunen et al. 2004b). Only a few species of bacteria are able to degrade methylene urea in soil. The bacterial species were isolated using traditional microbiological techniques, and almost all of them are potential plant and animal pathogenic bacteria, such as *Ochrobactrum anthropi* (Jahns et al. 1997), *Ralstonia paucula* (Jahns et al. 1999; Jahns and Kaltwasser 2000), and *Agrobacterium tumefaciens* (Koivunen and Horwarth 2004). These bacteria synthesize enzymes capable of hydrolyzing methylene urea to a form of N available to the plants. The enzymes are all classified as MDUase (EC 3.5.3.21; methylenediurea deaminase) but each appears different for each bacterial species. In *Ralstonia* sp., the enzyme is a gene fusion between a urease (EC 3.5.1.5) and a protein family of unknown function. Nevertheless, the sequences of the chemical reactions are the same in all cases, and methylene urea hydrolysis leads to three different products, formaldehyde, urea, and ammonium.

To improve the NUE of plants and diminish N losses by leaching and run off, it is important to understand the process responsible for degradation of methylene urea (Koivunen et al. 2004a; Koivunen and Horwath 2004). There is little information about the microbial populations involved in biodegradation of methylene urea in soil, although some microorganisms that degrade dimethylurea have been isolated. There is no information concerning the conditions that influence the transfer of mixed microbial populations that enhance the degradation of dimethylureas from one soil to another. Since the microorganisms isolated were all potential plant pathogens, it is important to elucidate the long-term abiotic and biotic mechanism triggered by this type of fertilizer (Garcia-Teijeiro et al. 2009).

Soil quality before and after the use of these N fertilizers should be compared by physical, chemical, and biological methods (Garcia-Teijeiro et al. 2009). All three approaches detect specific soil characteristics as well as possible interactions and thus can reflect changes in soil quality. Biomass, community structures, and specific functions of soil microorganisms appear to be of major importance for general soil functions and could serve as sensitive soil quality indicators. The microbiological characteristics of a soil reflect and integrate chemical, physical, and biological soil properties over time, since microbial soil communities strongly depend on the conditions of the habitat they colonize. Therefore, microbiological characteristics of a soil may provide indicators, which integrate short-, middle-, and long-term changes in soil quality. As soils display a multitude of biological characteristics and many of them may not be accessible, specific indicators have to be chosen (Zhao et al. 2005).

Nodule Effects

A surprising observation has been that nodules and N_2 fixation reduce legume yield and water use efficiency (WUE) in some genotypes (Sinclair et al. 2007; Valentine et al. 2011). Consequently, as breeders pursue high grain yields, they may have been inadvertently selecting against nodulation and limiting N_2 fixation. In some cases, N fertilizer is applied to legume crops, which will inhibit nodule formation because nodulation and nodule development are heavily suppressed when nitrate is present. New genetic resources have been found that provide for yield and N_2 fixation during drought stress (Sinclair et al. 2007). Breakthroughs in understanding the molecular control of nodule formation (Indrasumunar et al. 2011; Indrasumunar et al. 2012) have also shown that these genes are special derivatives of genes altering the microbial community around roots. Future studies matching root genotypes to microbial populations can potentially provide significant improvements in NUE in future.

Drought Tolerance and Nitrogen Use Efficiency

The importance of drought tolerance and WUE to adaptation to climate change is discussed in detail by Ortiz and Siddique, respectively, in this volume. However N and water interact strongly to determine crop productivity (Sadras 2005) and water availability and the severity of drought can affect NUE. Drought tolerance genes contribute to greater NUE because they improve biomass production over an extended range of soil moisture availability and weather conditions (Pennisi 2008; Harrigan et al. 2009). Effective genes, including *NF-YB1* (Nelson et al. 2007), *CspB* (Castiglioni et al. 2008), and *gdhA* (Mungur et al. 2006; Lightfoot et al. 2007), signal the cell and plant to maintain photosynthesis when water first becomes limiting and help photosynthesis recover quickly when water supply improves. Glutamate is an amino acid implicated in signaling and homeostasis because of the close regulation of cellular concentrations (Forde and Lea 2007). Using it, drought-tolerant crops were produced first in tobacco (Ameziane et al. 2000; Mungur et al. 2006) then in maize (Lightfoot et al. 2007). What was most interesting about the plants was that although total free amino acid concentrations doubled, glutamate did not, leading to the hypothesis that the drought tolerance was caused by signaling of sufficiency that caused an increase in compatible solutes. Metabolite analyses (Nolte et al. 2004; Mungur et al. 2005; Nolte 2009) showed that many hundreds of metabolites changed in abundance in shoots and roots. In addition, changes in crops can have beneficial side effects on plant pathogen interactions (Lightfoot and Fakhoury 2010). Therefore, the NUE/WUE technologies have promise for use during dry spells in agricultural production.

10.5.2.2 Genomic Approaches

Use of *Arabidopsis* Mutants

Gene function identification by mutagenesis of *A. thaliana* is an established protocol, and hundreds of mutant genes in a variety of plant processes have been defined, mapped, and some isolated (Huala et al. 2001). The recent development of TILLING programs for many crops (Cooper et al. 2008) promises an abundant supply of new mutants. Mutants in mineral nutrition, root development, and disease resistance have been isolated and mapped in *Arabidopsis*. Gene isolation by positional cloning has been reported for many mutated genes. However, mutants of relevance to NUE are rare (see Table 11.1); only the assimilation enzymes, gluR, and gsr1 lesions have been reported. Reviewing these will be informative.

Mutants in GS and GOGAT are lethal because of the fluxes through photorespiration (see review by Forde and Lea 2007). The two mutants in the mitochondria-located NADH-dependent GDH paralogs tend to be less resistant to abiotic stresses in both *A. thaliana* and *Zea mays* (Lea and Miflin 2011). Mutants in the NADPH GDH enzymes found in plant plastids and cytosol do not have clear phenotypes (Frank Turano, personal communication 2011). Mutants in aspartate and asparagine synthesis and transport are deleterious, underlining their role in transport and storage (Vidal et al. 2010). Double mutants in nitrite reductase are lethal because nitrite is very toxic whereas single mutants are phenotypic. In contrast, single mutants in nitrate reductase have either a neutral effect or can increase NUE. Kleinhofs et al. (1980) showed that barley with 10 % of the usual nitrate reductase activity was just as productive as the wild type. This phenomenon has been repeated in other plants. Nitrate reductase production by plants far exceeds the needs of a well-fertilized plant, which is probably a holdover from the predomestication era. Reducing the metabolic load of high nitrate reductase production may increase NUE.

Two regulatory mutants were well characterized. Gsr1 was a lesion that caused increased susceptibility to methylamine (Meyer 1997; Meyer et al. 2006). Different N sources provided different degrees of protection from the toxicity of methylamine. Glutamine was more protective than glutamate, nitrate, and nitrate mixed with ammonium more than ammonium. The lesion in gsr1 interfered with photosynthesis, emphasizing the control of C metabolism by the plant's N status. The lesion in gsr1 appears to map to a region of chromosome 5 encoding an amine oxidase, suggesting a mechanism for the lesion in detoxification. Lesions in putative glutamate receptors are known (Lam et al. 1998; Dennison and Spalding 2000; Coruzzi and Zhou 2001). These lesions provide alterations in growth and NUE as well as tolerance of second messaging inhibitors like okadaic acid. However, some mutants have unusual genes underlying N-regulatory like phenotypes (Godon et al. 1996) suggesting the field will continue to be recalcitrant to analysis.

Several transporters in plants and their microbial symbionts provide for alterations in NUE because all forms of N are accumulated against a steep concentration gradient (Godon et al. 1996; Kaiser et al. 1998; Gupta et al. 2011). Ammonium in particular is hard to accumulate and may pass in and out of cells several times before assimilation is successful. Consequently lesions in ammonium and nitrate transport are deleterious and do not improve NUE. The lesion in proton-dependent peptide transport is different. Resistance to herbicides targeted to the enzyme GS like MSX is provided by the lack of these transporters and NUE can be increased. These transporters will be particularly important to assimilating fertilizer N from root-associated microbes.

Microarrays and Transcript Analysis

Large numbers of genes are being discovered to be involved in processes like NUE by clustering during microarrays in crop plants. To obtain functional information on these genes, efficient expression monitoring methods have been developed (Wang et al. 2000). Rapid and simultaneous differential expression analysis of independent biological samples indicates activity. Using expression profiles, gene regulation perturbations in transgenic and mutant plants can be monitored and function inferred providing a central platform for plant functional genomics (Schenk et al. 2000; Wang et al. 2000). However, microarrays of relevance to NUE are rare: only gsr1 and a few enzyme lesions have been reported.

Microarrays have led to the patenting of sets of protein families implicated in NUE (Table 10.5). For example, Goldman et al. (2009) have applied for a patent for 157 protein families implicated in NUE by microarray and then tested for activity in transgenics which resulted in one or more positive results from assays of NUE,

Table 10.5 Partial list of protein families implicated in nitrogen use efficiency by "-omics" approaches

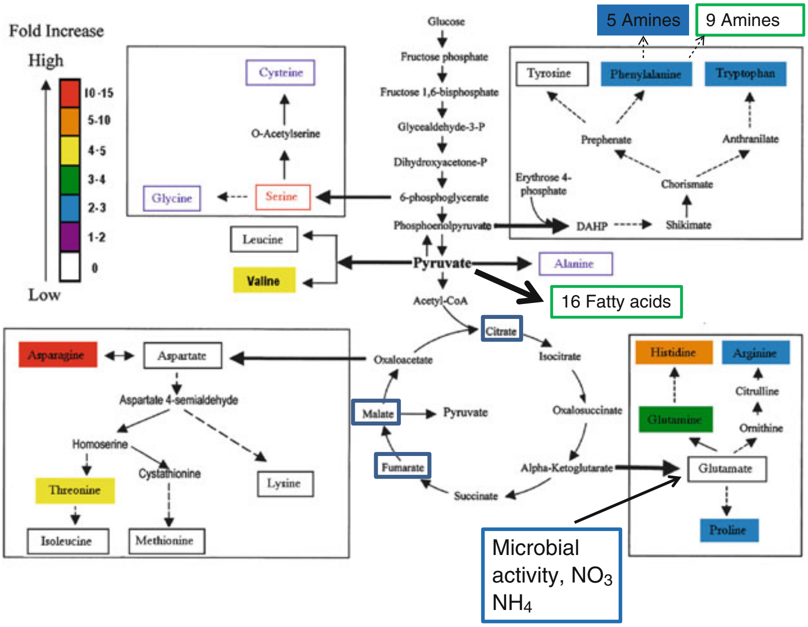
ADH_N	ADH_zinc_N	AP2	AUX_IAA
Aa_trans	Acyl_transf. 1	Aldedh	Aldo_ket_red
Alpha-amylase	Aminotran1-3	Ammonium_transp	Arm
Asn_synthase	BAG	BSD	Beta_elim_lyase
Biotin_lipoyl	Brix	Bromodomain	C1$_4$
CTP_transf2	Catalase	CcmH	Chal_sti_synt_C
Cyclin_C	Cyclin_N	Cys_Met_Meta_PP	DAO
DIM1	DPBB1	DRMBL	DUF167
DUF231	DUF250	DUF6	DUF783
DUF962	E2F_TDP	E3_binding	EBP
Enolase_C	Enolase_N		

WUE and yield, in enhanced tolerance to salt, cold and heat, and in enhanced concentrations of oil and/or protein in seed.

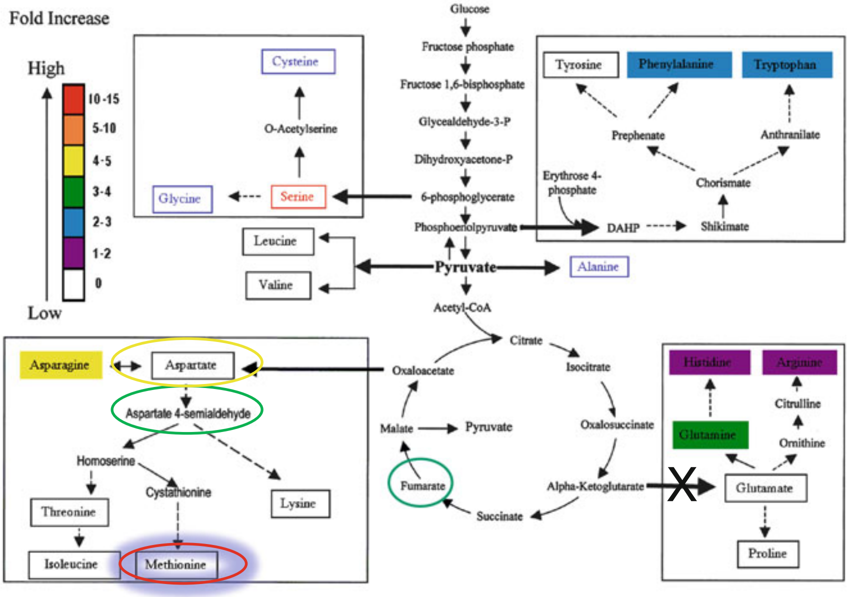
Metanomic Tools for Extending Functional Genomics

In the postgenome sequence era, the determination of gene function(s) and relationships to pathways will be the focus. Multiparallel analysis of mRNA abundance and their protein products will suggest functions but not direct information on biological function. The multiplicity of gene interactions and metabolic network changes engineered by mutation are not always predictable, and many changes are cryptic. Metabolic profiling can link phenotype to biochemistry (Mungur et al. 2005; Nolte 2009). The methods are fast, reliable, sensitive, and automated due to improvements in mass spectrometry (MS). Libraries of compound identities have been developed for plants at mass accuracy of 0.01d, often by MS–MS fragmentation. However, the mass accuracy of ion cyclotron MS in a Fourier-transformed MS format provides for mass accuracy to 0.0001d. This accuracy allows for unequivocal identification of a larger number of compounds in fewer analyses.

Figure 10.8 shows the effects of GDH on pathways related to NUE in tobacco roots. FT-ICR-MS detected 2,012 ions reproducible in 2–4 ionization protocols. There were 283 ions in roots and 98 ions in leaves that appeared to significantly change abundance due to the measured GDH activity. About 58 % of ions could not be used to infer a corresponding metabolite. From the 42 % of ions that inferred known metabolites, many amino acids, organic acids, amines, and sugars increased and many fatty acids and amines decreased. These changes were profound and underlay the ability of the GDH transgene to increase NUE, ammonium assimilation, and nutritional value. The changes in core metabolism looked very similar to the changes reported for N-sink altered opaque mutants of *Z. mays*. The C skeleton map of Fig. 10.8 may not be the best way to look at the interactome. Two other views, the N fate map for N assimilation and the protein–protein interaction, are



Amino Acid Changes in Leaves without (boxes) and with (ovals) gluphosinate



Metabolites in blue boxes were not detected. Metabolites in red boxes were used as internal standards and therefore not measured. Metabolites in black boxes were detected and not changed. Glow indicated increased by gluphosinate

Fig. 10.8 Metabolite changes related to NUE in GDH transgenic roots (**a**) and leaves (**b**). Metabolites in *blue boxes* were not detected. Metabolites in *red boxes* were used as internal also useful. In all three views, it is clear that N assimilation is at the nexus of many pathways. In fact, pyruvate and glutamate are at the center of metabolism, being related by 2.7 metabolisms on average to the metabolites in the cell. Still it is surprising that modest changes in glutamate concentrations in the cytoplasm had so many effects. Equally surprising was the observation that the transcriptome was not altered (Mungur et al. 2005). It should be expected that analysis of the proteome and metabolome promises to identify new genes useful for altering NUE that are missed by mutation, overexpression, and TA screens.

Metabolic analysis was also applied to the alanine aminotransferase (AlaAT) transgenic plants with improved NUE (Good et al. 2004). Rice (*O. sativa* L.) was genetically engineered by introducing a barley AlaAT cDNA driven by a rice tissue-specific promoter (OsAnt1; Shrawat et al. 2008). This modification increased the biomass and grain yield significantly in comparison with control plants when plants were well supplied with N. Compared with controls, transgenic rice plants also demonstrated significant changes in key metabolites and total N content, indicating increased N uptake efficiency. Metabolites included many of those reported for GDH. Goldman et al. (2009) report similar effects from an alanine decarboxylase in transgenic plants.

Transgenics Lacking A Priori Evidence for Nitrogen Use Efficiency

Table 11.1 (Chap. 11) summarizes some recent examples of transgenic approaches lacking a priori evidence of involvement in NUE that have been used to improve NUE. These approaches also showed NUE and WUE are closely interrelated. The connection between C metabolism and N metabolism underlies this association. These protein family and gene lists are very interesting, being mixtures of assimilation enzyme transport factors and esoteric proteins. Proteins like gluconases, catalases, and lyases are hard to place in relation to known pathways underlying NUE. However, the preponderance of proteins involved in TA control and protein degradation provides clues to the effect. Regulatory pathways in plants are hierarchical with about three layers. The enzymes in the basal layer are each controlled by several middle layer regulators. In turn, these are regulated by a few proteins sensitive to key environmental cues. The relationships are reciprocal to a change in a lyase that might alter the activity of a protein in a well-characterized NUE pathway. However, caution is warranted since even well-defined enzymes like GS (Kichey et al. 2005; Kichey et al. 2006) and their alleles (Ortega et al. 2006) have

◀

Fig. 10.8 (continued) standards and therefore detected. Metabolites in *blue boxes* were increased 2–3 fold. Metabolites in *black boxes* were detected and not changed. Metabolites in *green boxes* were decreased. Metabolite circled were altered by gluphosinate treatments. (adapted from Mungur et al. 2005) complex relationships with plant growth and development (Hemon et al. 1990). Interactome analysis promises much in this area in the next few years.

10.6 Conclusions

Understanding of the control of NUE is at a new beginning (Krouk et al. 2010). Surprising effects of individual proteins abound showing our understanding of the processes behind NUE is preliminary. The potential for gain remains large. Most of the gradual increase in crop yield in major well-fertilized crops is likely an expression of NUE and WUE. However, to date the improvements in NUE provided by genes like GDH and AlaAT remain to be commercialized. The integrations of techniques made by systems biology hold promise. Can crop yields be moved on in quantum leaps by manipulating NUE? The very large yield gains from weed control provided by herbicide resistance technologies suggest NUE is improved in those crops. Can NUE be directly manipulated? If the soil's microbial community is considered and properly measured, that may finally be possible.

At the same time, as the need to increase in food production becomes greater, crops for biofuels are needed that do not compete with crops for food. Growth on marginal lands requires the second form of NUE—growth with low or no inputs. Here we must reverse centuries of crop breeding. The directed manipulation of NUE must be applied to both fields if this planet is to sustain a human population of nine billion by 2050.

10.6.1 Breeding for Improved Phosphorus Use Efficiency

After N, P is the second most important nutrient in crop production. Over half of the world's agricultural land has soils low in plant available P (Lynch 2011) and production relies on regular application of P fertilizer. In intensive systems in which regular applications of P occur, recovery of fertilizer P is low in the year of its application resulting in a gradual increase in soil P levels (Vance et al. 2003). The finite reserves of the world's supplies of high-quality rock phosphate have prompted concerns about the reliability of supplies in the future and have raised the specter of "peak phosphorus" (Cordell et al. 2009). There is a general consensus that improvements PUE are required and there is a need to explore the ability to improve crop PUE to limit further inputs of P (Hinsinger et al. 2011). In regions where soil P reserves have built up over time, improving the ability of plants to exploit soil reserves has been emphasized (Vance et al. 2003), although there is growing interest in improving the efficiency of utilization of P taken up by plants (Wang et al. 2010; Rose and Wissuwa 2012). However in regions where soil P levels are severely depleted, strategies to improve soil P will also need to be adopted in concert with genetic improvement.

Phosphorus in soil is poorly available to plants because of reactions with minerals such as aluminum, Fe, and calcium as well as being bound in organic matter. It also moves slowly to the root surface by diffusion. A low supply of P can induce a P starvation response to either enhance uptake from the soil or to maintain P homeostasis in actively growing tissue. There are many mechanisms that plants employ to increase uptake of P, including changes in root architecture; secretion of organic acids, protons, and phosphatases to increase the availability of phosphate in the rhizosphere; interactions with microorganisms; and symbiotic relationships with mycorrhizal fungi. These processes and their potential value to improvements in P nutrition have been extensively reviewed recently (Gahoonia and Nielsen 2004; Rengel and Marschner 2005; George and Richardson 2008; Kirkby and Johnston 2008; Richardson et al. 2009a, b). Low supplies of P may also lead to greater recycling of P within the plant from intracellular organic P compounds by increasing activities of APase PAPs, RNase, and scavenging Pi by replacing membrane phospholipids with galacto- and sulpho-lipids, which will contribute to greater PUE. However, under P starvation, it is important to distinguish between a general stress response and traits associated with improved tolerance to P stress to enable gains in PUE to be achieved (Pariasca-Tanaka et al. 2009).

The complexity of P nutrition of plants is because the availability and uptake of P depends on the interaction between soil, plant, and microbial processes and the plasticity afforded by increased recycling of P. Consequently, the relative importance of different processes and the effectiveness of different plant characteristics are likely to vary according to soil type, cropping history, and climate and weather. Therefore, targeting one specific mechanism to improve P uptake by plants may yield limited success. This is not to say that gains cannot be made as there have been reported improvements in PUE in a number of crops in China (Yan et al. 2006). However, a common thread among many studies is that the ability to take up P from small pools of available P in the soil is crucial to the P nutrition of crops. Therefore much of the interest in genetic improvement in PUE has centered on differences in genotypes being able to increase the availability P in soil and its uptake. Root traits have figured prominently in studies in PUE (Vance et al. 2003; Wissuwa et al. 2009).

At present conventional approaches to genetic improvement are being used to improve PUE, with QTL mapping and marker-aided selection being a particular focus. As our understanding of the physiological and molecular bases of P starvation responses and PUE improve, it is likely that genetic engineering will figure more prominently in future gains in PUE, although the success of a transgenic strategy will depend on public acceptance.

10.6.1.1 Current Challenges

While there has been a long history of characterizing genetic differences in NTUE among crop plants, breeding for improved NTUE is still in its infancy. The development of molecular technologies to understand the genetic basis of the trait and mechanisms of nutrient efficiency has provided new possibilities for significant advances to be made. Despite exciting opportunities, there are a number of challenges to improving PUE, whether based upon conventional genetic or transgenic approaches.

Incomplete Understanding of Controls of P Uptake

The growth and P uptake of a crop relies on a complex interaction between the plant, the chemical and physical characteristics of the soil, and the biological properties of the rhizosphere. While there have been significant advances in our understanding of specific components of this system and of their genetic basis, time and again the comment is made in reviews of P nutrition that our understanding of the operation of the system is incomplete. There are many examples of traits that result in substantial improvements in P nutrition under controlled conditions, which fail to show similar advantages in field soil. This is one of the compelling reasons for rigorous testing in soils that are representative of commercial practice.

Appropriate Phenotyping

Much of the reported work comes from glasshouse, controlled environment and hydroponic studies. This is out of convenience as well as necessity in the case of genetic modification (GM). There have been few studies in which results from controlled environment experiments have been compared with responses in field trials. Soil properties will influence the form and the availability of P but our understanding of the importance of specific mechanisms of PUE in different soils is poor. High-throughput screening methods are desirable, but if they cannot be demonstrated to correlate with results obtained from commercial growing situations, then their application may be limited.

Environmental Variability in Expression of Phosphorus Use Efficiency

Grain yields of rainfed crops show large environmental variation, which reflects differences in seasonal conditions. Variation in soil moisture is likely to play an influential role in the availability of soil P, P uptake, and the consequent expression of PUE. Such considerations have not been addressed adequately as there have been few long-term assessments of genetic diversity for PUE under field conditions. Identifying genotypes, which show consistent PUE over a range of environments, is a key element to identify traits to improve PUE.

Limited Population-Based Studies

A review of the studies presented in Table 10.6 suggests there are a limited number of population-based mapping studies. A larger number of mapping studies within species will provide greater certainty of the value of QTL regions detected, and common QTLs could then be targeted for map-based cloning and potential transgenic approaches to improve PUE.

10.6.1.2 Genomic Approaches

QTL and Marker-Aided Selection

PUE is a complex trait subject to considerable environmental influence. Identifying QTL for PUE and subsequently developing molecular markers have the potential to improve selection for high PUE in crops. However, despite the large number of QTLs that have been identified for a variety of traits, including PUE, few have been actively deployed in plant-breeding programs and are used routinely by plant breeders (Collins et al. 2008). Lack of field validation in a range of genetic backgrounds and over environments as well as the small effects of many QTLs are contributing factors for the lack of success. These are important issues that need to be addressed if marker-aided selection is to be used to improve PUE in crop and pasture plants. However increasingly, marker-assisted selection is being used routinely and this trend will continue into the future. For example, marker-assisted selection has contributed to the release of more than 90 % of the varieties of common beans released in the USA over the past decade (McClean et al. 2011).

Phosphorus Uptake and Phosphorus Use Efficiency

There are relatively few studies that have identified QTLs for PUE in the major crop species (Table 10.6). Generally, biomass production, shoot P concentration, and uptake are the traits of interest, and these are often assessed under both limiting and nonlimiting P conditions. Given the central role of biomass and yield in most definitions of PUE, it is not surprising that the QTLs for biomass and yield often collocate with QTLs for P uptake and/or P utilization efficiency. For example, in wheat (Su et al. 2006, 2009), *Brassica* sp. (Hammond et al. 2009; Yang et al. 2010, 2011), soybean (Zhang et al. 2009), and rice (Wissuwa et al. 1998), QTLs for P uptake efficiency collocated with QTL for biomass production. This is because the correlation between biomass production and shoot P uptake is often high and shows that biomass production drives P uptake. Many studies show that QTLs detected for P uptake are linked in repulsion with QTLs for PUE (Wissuwa et al. 1998; Su et al. 2006, 2009; Zhang et al. 2009) with the authors suggesting that it will therefore be difficult to improve both traits simultaneously. It is not clear if this negative correlation is an artifact of the definitions that are used for P uptake and PUE.

Table 10.6 Summary of studies that have identified QTL associated with phosphorus use efficiency

Population	Environment(s)	Population size	Marker no	Traits[a]	QTL no	Variation explained (%)	Reference
Wheat (*Triticum aestivum*)							
Lovrin10/Chinese spring	Glasshouse	92 DH lines	253	P uptake P utilization efficiency	39	5.7–34.6	Su et al. (2006)
Hanxuan10/Lumai14	Glasshouse and field	120 DH lines	395	P uptake efficiency P utilization efficiency	195	4.1–38.8	Su et al. (2009)
Barley (*Hordeum vulgare*)							
Association mapping panel	Field	120 (56 winter types; 64 spring types)	921 (winter) 843 (spring)	Shoot P concentration	8	Not provided	George et al. (2011)
Brassica sp./*Brassica napus*							
AD12DHd/GDDH33	Glasshouse	90 DH lines	Not provided (~90 % genome coverage)	Agronomic efficiency P uptake efficiency P utilization efficiency Physiological P use efficiency P efficiency ratio	37	5.3–52. 6	Hammond et al. (2009)
Eyou Changjia/B104-2	Greenhouse	124 RILs	503	P uptake	62	8.1–17.1	Yang et al. (2010)
Eyou Changjia/B104-2	Greenhouse	124 RILs	553	P uptake P use efficiency	71	Not provided	Yang et al. (2011)
Common bean (*Phaseolus* sp.)							
DOR364/G19833	Growth pouches and field	86 RILs (growth pouches) 71 RILs (field)	236	P acquisition efficiency	22	9.3–20.3	Liao et al. (2004)

DOR364/G19833	Field and greenhouse (hydroponic system)	71 RILs (field) 86 RILs (greenhouse)	236	P acquisition efficiency	26	9.4–51.3	Beebe et al. (2006)
G19833/AND696	Field	75 RILs	167	P uptake P use efficiency	29	9.0–33	Cichy et al. (2009)
Soybean (*Glycine max*)							
BD2/BX10	Field	106 RILs	296	Root and shoot P concentration	31	9.1–31.3	Liang et al. (2010)
Nannong94-156/Bogao	Greenhouse	152 RILs	371	P acquisition efficiency P use efficiency	34	6.6–19.3	Zhang et al. (2009)
Rice (*Oryza sativa*)							
Nipponbare/Kasalath	Glasshouse	98 BILs	245	P uptake P use efficiency	7	5.8–27.9	Wissuwa et al. (1998)

[a] For clarity, only phosphorus use efficiency-related traits (and not each of the component traits) are reported in the table

If a genotype has a high P uptake efficiency (driven by biomass production), its P utilization efficiency (calculated as biomass production per unit P uptake) will be low. This further highlights the problem with commonly used definitions of NTUE.

An alternative, but infrequently used, approach is to examine QTLs for relative yield under low and high supplies of P to overcome the potential confounding effect of high biomass or yield on P uptake and PUE. Yang et al. (2010) assessed the relationship between QTLs for root traits and P uptake in *Brassica napus* and found that QTLs for P uptake and biomass production were linked. Later, they used relative yield and state that "these QTL were demonstrated to represent the true QTL for P efficiency" (Yang et al. 2011). Unfortunately the two sets of results cannot be directly compared due to the different format in which the maps were presented.

Currently some of the most promising works on breeding for improved PUE is in rice, where a QTL associated with P uptake (*Pup 1*) has been identified and found to confer significant improvements in growth and yield in upland rice under low soil P (Wissuwa et al. 1998; Chin et al. 2010, 2011). The identification of the QTL was based on growth under severely P-deficient conditions. Subsequent germ plasm surveys have shown that the P efficiency allele at *Pup 1* was most commonly found among genotypes developed for drought-prone, hostile upland environments (Chin et al. 2010). Interestingly, it seems that the value of *Pup 1* to PUE is not associated with genes directly related to P uptake and the underlying mode of action of *Pup 1* is yet to be described. The candidate genes associated with the QTL include a protein kinase gene and a dirigent-like gene that have been reported to be involved in root-specific growth functions and in tolerance to abiotic stress and a hypothetical gene that also has a root-specific function (Chin et al. 2011).

Root Traits

Another area of work that has shown promise in a number of crops is root architecture. To maximize P acquisition in low P conditions, plants change root growth and development by promoting the formation of a shallow, highly branched root system through a reduction of primary root growth and an increase in adventitious roots and lateral root density as well as the development of more and longer root hairs. Root architectural traits associated with enhanced topsoil foraging include shallower growth angles of axial roots, a greater number of adventitious axial roots, and greater dispersion of lateral roots (Péret et al. 2011). A number of genes controlling lateral root development have been identified in *Arabidopsis* (Péret et al. 2011) and rice (Coudert et al. 2010). At least six root QTL have been identified in maize and are good candidates for further evaluation (Hund et al. 2011). Genetic variation in root hair length and loci-controlling barley root hair formation has also been identified (Gahoonia and Nielsen 1997; Szarejko et al. 2005).

There have been a number of attempts to link QTLs for root development and architectural traits with QTLs for P uptake or utilization efficiency (Liao et al. 2004;

Beebe et al. 2006; Ochoa et al. 2006; Cichy et al. 2009; Hammond et al. 2009; Zhang et al. 2009; Liang et al. 2010; Yang et al. 2010, 2011). Common bean (*Phaseolus vulgaris* L.) has been the most widely studied species in this respect. When P is concentrated in the topsoil, lines of beans with shallow rooting were more productive than lines with deep roots (Rubio et al. 2003). Subsequent work used a population developed from a cross between Andean and Mesoamerican parents in which Beebe et al. (2006) and Liao et al. (2004) analyzed the same field data set either with hydroponic screening (Beebe et al. 2006) or growth pouch results (Liao et al. 2004). Three of the QTLs that contributed to P acquisition efficiency (*Pup4.1*, *Pup7.1*, and *Pup11.1*) in the field were linked to some of the QTLs associated with root gravitropism in growth pouches (Liao et al. 2004), suggesting root gravitropism contributes to PUE. Beebe et al. (2006) reported fewer QTLs for P acquisition efficiency in the field, but nevertheless, some of the QTLs for root architectural traits identified in the field and in hydroponics were associated with P acquisition QTLs (Beebe et al. 2006). Ochoa et al. (2006) examined adventitious root formation in a related population but the QTLs for adventitious root formation were not located in the same region as the QTLs for P acquisition efficiency as reported in Beebe et al. (2006) and Liao et al. (2004). Cichy et al. (2009) also could not find any relationship between root traits and P uptake in an Andean/Andean bean population. The contrasting results for the relationship between root architecture and PUE in these studies reflect the difficulty in phenotyping root architectural traits and the small effect of the QTLs that have been identified.

The Influence of Phenology

Crop phenology is an important influence on nutrient uptake and allocation and may play an important role in adaptation to low availability of soil P (Nord and Lynch 2009; Nord et al. 2011). The importance of phenology is also highlighted in a number of genetic studies, although it is unclear whether these associations are a result of the effect of P deficiency on development or play a role in PUE. In wheat, Su et al. (2006) identified a range of QTLs associated with P-deficiency tolerance, with three main clusters located on chromosome 4B, 5A, and 5D. Interestingly, the 5A and 5D QTLs were associated with the major vernalization genes, *Vrn-A1* and *Vrn-D1*. In a later study on a different wheat population, the effect of *Vrn-A1* and *Vrn-D1* were not detected, but it is unclear if this population was segregating at these loci (Su et al. 2006). In barley, George et al. (2011) attempted to identify QTLs for shoot P concentration in an association mapping panel of 120 barley genotypes, composed of 56 winter and 64 spring types. No common QTLs could be detected between winter and spring types. However, the associations only just exceeded the threshold for detection, and George et al. (2011) attribute this to the relatively small population sizes that were used for the study and/or limited genetic variation. QTLs for PUE in common bean were linked with the *fin* gene, which regulates determinism in this species (Cichy et al. 2009).

There are not enough studies of different populations within a species to make a strong case for the likely effectiveness of any particular QTLs that have been detected. A further issue arises from the population sizes that are used in many studies. The effect of population size on the accuracy of QTL mapping is well known; in small populations, only QTLs with large effect are likely to be identified, and their effect can be overinflated (Tanksley 1993). The small population sizes that are generally used probably arise from difficulty in phenotyping for PUE since the need to screen at both limiting compared to nonlimiting conditions doubles the amount of phenotyping that needs to be done.

A review of the studies presented in Table 10.6 suggests clear directions that should be taken for future QTL-mapping studies. Identification of QTLs under controlled conditions does not necessarily mean that the QTLs will be of practical value to plant breeding. A larger number of mapping studies within species will provide greater certainty of the value of QTL regions detected, and common QTLs could then be targeted for map-based cloning and potential transgenic approaches to improve PUE. Use of near isogenic lines to assess the effect of the QTLs will also be valuable. The effect of the QTLs also needs to be demonstrated under field conditions to examine the influence of the QTLs, and ideally, screening for PUE should be conducted on a range of different soil types and environments. Problems associated with definition of PUE need to be overcome—a comparison of results obtained using different definitions will help. Finally, the phenomenon of linkage of developmental genes with PUE should be investigated further to determine if certain combinations, particularly in wheat, can lead to improved PUE.

Transgenic Approaches for Improving Phosphorus Use Efficiency

The use of molecular breeding to improve PUE is in its infancy. However, in the long-term, engineering key components in the regulatory network of the P starvation response represent a useful approach for molecular breeding of plants toward more efficient Pi uptake and use. This has been shown in *Arabidopsis* and rice using overexpression and gene knockdown or knockout. Artificial target mimics of miRNAs can also be used for functional studies on PSR and has potential to contribute to molecular breeding. Table 10.7 provides an overview of genes that have been assessed using transgenic approaches and Table 10.8 provides detail of the promoters that have been used to control gene expression.

Overexpression

Overexpression of the high-affinity OsPHT1;8 increases Pi uptake and translocation from roots to shoots in rice (Jia et al. 2011) although no increase in Pi uptake has been seen in barley (Rae et al. 2004). Transgenic rice lines overexpressing OsPHT1;8 increased maximum influx by 3–5-fold, indicating the transgenic approach can enhance Pi uptake from soil in this crop (Jia et al. 2011).

Table 10.7 Potential genes for enhanced phosphorus uptake and remobilization

	Function	Source	Background	Promoter	Phenotype	Reference
P uptake						
OsPHT1;8	High-affinity Pi transporter	Rice	Rice	Maize ubiquitin	P uptake, P translocation to grain	Jia et al. (2011)
ALMT1	Malate transporter	Wheat	Barley	Ubiquitin	P uptake	Delhaize et al. (2009)
AVP1	Root proliferation, apoplast acidification	*Arabidopsis*	*Arabidopsis* Tomato Rice	AVP1	P uptake, root size	Yang et al. (2007)
P translocation						
OsPHT1;2	Low-affinity Pi transporter	Rice	Rice	Ubiquitin	P translocation	Liu et al. (2010)
AtPHT1;5	Pi transporter	*Arabidopsis*	*Arabidopsis*	Actin	P translocation	Nagarajan et al. (2011)
Transcription factors						
PHR1	MYB transcription factor	*Arabidopsis*	*Arabidopsis*	CaMV 35S	P uptake, translocation Root proliferation	Nilsson et al. (2007)
PHR2	MYB transcription factor	Rice	Rice	CaMV 35S	P uptake, translocation, root length	Zhou et al. (2008)
miRNAs and other genes						
Target gene						
miR399	Ubiquitin conjugase E2	*Arabidopsis* Rice	*Arabidopsis* Rice		P uptake, root to shoot transfer	Aung et al. (2006), Hu et al. (2011)
MiR399d	Ubiquitin conjugase E2	*Arabidopsis*	Tomato	CaMV 35S	P uptake Acid phosphatases	Gao et al. (2010)
PHO2	Unknown	Rice	Rice	mutation	P translocation	Hu et al. (2011)

Table 10.8 Tissue-specific and P-inducible promoters in plants

Gene	Source	Expression patterns	Tissue specificity	Reference
AtPHT1;5	*Arabidopsis*	P deficiency	Source to sink	Nagarajan et al. (2011)
HvPHT1;1	Barley	P deficiency	Epidermal, cortex, and stele of roots	Schunmann et al. (2004)
HvPHT1;2	Barley	P deficiency	Epidermal, cortex, and stele of roots	Schunmann et al. (2004)
OsPHT1;8	Rice	Constitutive	Roots and shoots	Jia et al. (2011)
OsIPS1	Rice	P deficiency	Phloem	Hou et al. (2005)
MiR399	*Arabidopsis*	P deficiency	Phloem	Aung et al. (2006)

Overexpression of miR399s leads to a reduction in remobilization of Pi in *Arabidopsis* (Aung et al. 2006) and rice (Hu et al. 2011). This approach has also been used to modify secretion of acid phosphatase and protons in the roots of tomato, which facilitated the hydrolysis of soil organic P and dissolution of Pi (Gao et al. 2010).

Gene Knockdown and Knockout

Knockdown OsPHT1;8 reduced Pi uptake and translocation (Jia et al. 2011). Knockout of *Osphf1* reduced Pi uptake and translocation from roots to shoots in rice as well as arsenate (Wu et al. 2011). The knockout mutant of *ltn1*, an ortholog of AtPHO2, shows several typical Pi-starvation responses, such as stimulation of phosphatase and RNase activities, lipid composition alteration, and N assimilation repression (Hu et al. 2011). The elongation of primary and adventitious roots is also enhanced in the *ltn1* mutant, suggesting that the modification of LTN1 expression may be able to enhance morphological, physiological, and biochemical responses to Pi starvation.

Cell-Specific Expression in Roots

Specific expression driven by cell-specific promoters instead of constitutive promoters will be preferred in some cases. Phosphatases that release P from organic compounds would be more useful if produced by shallow roots than by deep roots, since soil organic matter typically decreases with depth (Lynch 2011). In contrast, carboxylates capable of releasing P from Fe and Al oxides may be more useful when released into deeper soil horizons where these forms of P predominate (Lynch 2011).

10.6.1.3 Mycorrhizal Associations

The reduction in concentration of shoot P at elevated CO_2 concentrations can often be alleviated by the formation of AM symbioses (Cavagnaro et al. 2011). Therefore, the importance of mycorrhizal fungi may increase in the future in attempts to reduce the rates of P fertilizer applied to crops. Genetic variation for AM associations has been demonstrated in a number of plant species (Baon et al. 1993; Zhu et al. 2001; Jakobsen et al. 2005; An et al. 2010), which offers the potential to select for AM responsiveness. However, the positive effect of mycorrhizal colonization decreases as soil P levels increase, and further work would benefit from assessment of colonization at P levels that are representative of agricultural soils. Understanding the physiological and genetic controls of the AM–plant interaction may enable root infection to occur even at high soil P concentrations, which may enhance P uptake over a wider range of soil P concentrations than occurs currently. Also a better understanding of the genetic controls of AM infection and P uptake and nutrition of the host plant is required to allow the synergistic relationship to be manipulated.

10.7 General Conclusions

An adequate and balanced supply of essential nutrients is a cornerstone of improvements in crop productivity. Nutrient efficiency will become increasingly important in the future as farmers strive to achieve higher levels of productivity and maintain profitable enterprises in the face of increasing fertilizer prices and under the influence of a changing climate. The effects of climate change on soil nutrient cycling, nutrient availability, and crop nutrient requirements are difficult to predict. However, the principles that have governed efficient nutrient management in the past are not going to alter with future changes in climate. Nutrient management under a changing climate is likely to operate within the same boundaries as current practices.

The strategies to improve NTUE will differ depending on past nutrient management practices. In regions of the world where crops are chronically malnourished, increases in soil fertility through soil improvement and fertilizer use will underpin increases in productivity, while in areas where fertilizer has been applied in excess of the crops' requirements, better use of the soil nutrient bank and a more sustainable use of fertilizer will be needed. In both cases, breeding for improved NTUE can play an important role in increasing the NTUE of the system, although the specific breeding objectives to achieve this may differ.

There is considerable variability in how crop species and varieties exploit soil nutrients and respond to fertilizer. The improvements in yield potential that have been achieved by breeding have resulted in a passive improvement in NTUE, but there are few examples of commercial varieties being developed for their high

NTUE. The complexity of the soil and plant processes that influence the nutrient status of crops, the incomplete understanding of the genetic control of NTUE and its underlying physiological and molecular basis, and a consistent conceptual understanding of NTUE have limited progress.

The rapid development of an array of molecular and genomic techniques provides an opportunity to overcome many of the hurdles that have hindered progress so far. Plant scientists are at the cusp of making considerable advances in understanding NTUE and developing varieties that are more nutrient efficient. However, an important aspect of the use and implementation of this approach is that material needs to be tested under realistic field conditions. Marshaling new methods and technologies with the traditional disciplines of plant breeding, crop physiology, and agronomy provides expanded opportunities to study genetic differences in NTUE and to link genotype to phenotype (Andrade et al. 2009; Messina et al. 2009).

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