CHAPTER 17

Nitrogen and Phosphorus Use Efficiency[1]

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The improvement of nutrient use efficiency in wheat cropping systems can be achieved through two main strategies: by adopting more efficient crop management practices (such as nutrient rate, timing, source, and placement) and breeding more nutrient use efficient cultivars. Although both are important, this paper will focus on improving nutrient use efficiency (specifically, of nitrogen and phosphorus) through plant breeding. More detailed guidelines on how to improve nitrogen use efficiency in wheat through crop management have been described elsewhere (OrtizMonasterio,2001).

It is important to clearly define nutrient use efficiency before describing methods for improving it. We have found the definition proposed by Moll et al. (1982) useful in looking at genetic differences in nitrogen use efficiency among wheat cultivars. (Though the concept was developed using nitrogen as an example, it can also be applied to phosphorus.) These authors define nitrogen and phosphorus use efficiency in wheat as grain yield per unit of nutrient supplied (from the soil and/or fertilizer). They divide nutrient use efficiency into two components: uptake, or the ability of the plant to extract the nutrient from the soil, and utilization efficiency, or the ability of the plant to convert the absorbed nutrient into grain yield. Hence

Nutrient use efficiency = Uptake efficiency x Utilization efficiency

$$\frac{Gw}{Ns} = \frac{Nt}{Ns} \times \frac{Gw}{Nt} \qquad (1)$$

where Gw = grain dry weight, Nt = total above-ground plant nutrient at maturity, and Ns = nutrient supplied. All units are in g m-2. Utilization efficiency can also be subdivided into two components, as suggested by Ortiz-Monasterio et aI., 1997a, and expressed as follows:

Utilizotion efficiency = Harvest index x Nutrient biomass production efficiency

$$\frac{Gw}{Nt} = \frac{Gw}{Tw} \times \frac{Tw}{Nt} \qquad (2)$$

where Tw = total above-ground plant dry weight at maturity.

Utilization efficiency can also be expressed as:

Utilization efficiency = Harvest index x Inverse of total nutrient concentration in the plant

$$\frac{Gw}{Nt} = \frac{Gw}{Tw} \times \frac{1}{Nct} \qquad (3)$$

where Nct = total nutrient concentration in the plant as a percentage.

The definition for nitrogen use efficiency proposed by Moll et. aI. (1982) can be used for both low and high input situations. However, there are other nutrient efficiency classification systems that take into account performance both in the presence and in the absence of nutrient stress as, for example, the system proposed by Gerloff (1977), which separates cultivars into four groups based on their response to P. The groups are 1) efficient, responder; 2) inefficient, responder; 3) efficient, non-responder, and; 4) inefficient, non-responder. An efficient cultivar has higher yield than the other cultivars under low nutrient supply, while a responder cultivar has higher yield under high nutrient supply. This classification groups cultivars based on performance under low (efficient vs. inefficient) and high (responder vs. non-responder) nutrient supply, and allows the identification of those cultivars with adaptation to a range of soil nutrient conditions.

CIMMYT and its predecessor have been generating wheat germplasm for the developing world since the 1940s. CIMMYT bread wheats were first and most rapidly adopted in irrigated areas of the developing world (e.g., the Yaqui Valley in Mexico, the Indian Punjab, and the Pakistani Punjab) (Byerlee, 1996). Fertilizer is widely applied (sometimes at sub-optimal levels) by farmers in those areas as a way to correct nutrient deficiencies. However, in other target environments farmers do not apply

1 This chapter does not attempt to make an exhaustive review of the literature but rather presents practical information based on CIMMYT Wheat Program experience working on nitrogen and phosphorus use efficiency.

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fertilizers because they cannot afford them or because inputs are simply not available. It is thus essential that CIMMYT wheats be widely adapted and able to grow in different (low and high) soil nutrient situations.

In this chapter we will discuss how studying the individual components of nutrient use efficiency (uptake vs. utilization) under different nutrient levels can help us gain a better understanding of the opportunities and limitations of breeding for nitrogen and phosporus use efficiency.

Nitrogen

With the adoption of the input-responsive and lodging tolerant semidwarf wheat cultivars that launched the green revolution in the 1960s, the use of nitrogen fertilizer rapidly increased, as did yields. Thanks to the introduction of the new genetic material, the amount of grain produced per unit of N applied has increased significantly (Figure 1).

We have documented the changes in the nitrogen use efficiency of CIMMYT bread wheats developed between 1950 and 1985 under medium to high levels of

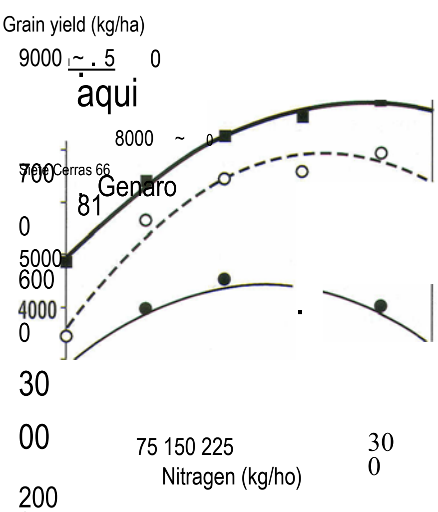


Figure 1. Response of tall (Yaqui *SO)* and semidwarf spring wheat cultivars to increasing levels of nitrogen fertilizer.

N fertility. Results show that more recent CIMMYT cultivars out yield both earlier semidwarfs and old tall cultivars at all nitrogen levels (Ortiz-Monasterio et aI., 1997a). This indicates that the current strategy of selecting and evaluating under medium to high N levels has resulted in germplasm that produces higher yield when grown under low or high levels of N fertility. CIMMYT bread wheats from 1950 to 1985 gradually became not only more responsive to N inputs, but also more efficient in their use, according to Gerloff's classification (1977). As a result, CIMMYT bread wheats do not require more N than the old tall cultivars; in fact, they often need less N to produce the same yield. In addition, since CIMMYT bread wheats are more responsive to N application, the optimum economic rate is higher than that for the old tall cultivars (OrtizMonasterio et aI., 1997a).

Although our current breeding strategy has been successful in addressing the needs of both low input and high input wheat-producing environments, we are interested in identifying alternative selection methods that might be even more successful. To that end, we characterized relevant CIMMYT germplasm for two main components of nitrogen use efficiency: nitrogen uptake and utilization efficiency. We found that there is genetic diversity for both traits.

Our work and that of others has shown that the level of N in the soil plays a very important role in the expression of uptake and utilization efficiency (Dhugga and Waines, 1989; OrtizMonasterio et al. 1997a). However, the effect of different soil N levels on the expression of a given component of nitrogen use efficiency in spring wheat may be affected by genotype and/or location. Dhugga and Waines (1989) found better expression of uptake efficiency under high soil N and better expression of utilization efficiency under low N. In contrast, Ortiz-Monasterio et al. (1997a) found better expression of uptake efficiency under low N conditions and better expression of utilization efficiency under high N conditions. These findings notwithstanding, available information has shown that the level of soil N may be manipulated together with genetic variability to develop cultivars with improved performance under both low and high input conditions (OrtizMonasterio et aI., 1997a; van Ginkel et aI., 2001).

Nitrogen uptake V5. utilization eHiciency

In view of the above, an important aspect of our current research is to identify the best selection strategies for developing genotypes that produce higher grain yields as a result of their improved uptake and/or utilization efficiency. The question is which component to emphasize.

Utilization efficiency has ecological appeal, since it means either higher yields with the same nutrient levels in the plant or the same yield with lower nutrient levels in the plant, which requires fewer resources. As indicated earlier, utilization efficiency can be broken down into harvest index and biomass production efficiency. If we analyze which component has been most associated with utilization efficiency gains in the past, we find that most progress has been associated with improvements in harvest index (HI) rather than in biomass production efficiency (Eq. 2). However, Fischer (1981) and Ca1derini et al. (1995) suggest that the possibilities of further improving HI as a way to increase grain yield are limited.

There are two main routes for making further progress in grain yield through better utilization efficiency: 1) to increase grain yield while maintaining or reducing nutrient concentration in the plant, and 2) to reduce total nutrient concentration in the plant while increasing or maintaining grain yield (Eq. 2). Most CIMMYT high yielding wheats grown under a wide range of N levels tend to have, on average, a nitrogen harvest index of around 75%. In other words, 75% of the plant's total N is found in the grain at maturity. This means that cultivars with higher utilization efficiency, which is not associated with HI (assuming a constant HI), will have lower protein concentration in the grain. This can negatively affect the grain's bread making quality and nutritional value, unless the percent protein reduction is compensated for by a proportional improvement in protein quality.

We should point out that bread making quality, which is a key issue for breeding programs in the developed world, is now gaining significance for breeding programs in developing countries. The original focus of many wheat breeding programs in developing countries-i.e., generating sufficient yield increases to feed their rising populations-has expanded to include fulfilling farmers' need to produce high quality grain that competes well on the market.

The nutritional value of wheat grain is another issue that is gaining in significance due to its perceived potential to better the nutrition of developing country populations. The nutrient content of wheat grain is negatively affected by lower protein concentration in the grain. Studies in Mexico and Argentina have shown that protein concentration in the grain has decreased as grain yield has increased throughout the history of breeding (Ortiz"Monasterio et aI., 1997b; Calderini et aI., 1995). This reduction in protein N has been associated with higher utilization efficiency. Thus an important challenge for breeding programs in both developed and developing countries will be to continue to improve nitrogen use efficiency and, at the same time, maintain or improve the bread making quality and/or nutrient content of wheat grain.

A similar dilemma arises when uptake efficiency, the other component of nutrient use efficiency, is implemented as a strategy to improve grain yield. For resource poor farmers who cannot afford fertilizers and grow wheat under low input conditions, the development of cultivars with high N uptake efficiency may not be desirable because it may accelerate soil nutrient mining. In contrast, in high input environments, high uptake efficiency is a very desirable trait because residual soil N (soil N not absorbed by the crop) may either leach through the soil to pollute waterways with soil nitrates or escape into the atmosphere as N_2, N_2O, NO_x' or NH_3'

Nitrate leaching has been well documented in many developed countries (CAST, 1985; Keeney, 1986). The problem tends to be associated with the application, especially in sandy soils, of more nitrogen than is required for producing maximum yield. Until recently, total N fertilizer use in the world was almost evenly divided between developed and developing countries from a total of 80 Tg y-! (FAO, 1990). However, the use of N fertilizer has been accelerating in the developing world. Of the 60-90% increase in global application of N fertilizer estimated to take place by 2025, two thirds will occur in developing countries (Galloway, 1995).

There are wheat production systems in the developing world where very high rates of N fertilizer are already being applied-for example, in certain wheatgrowing areas of Mexico and Egypt. In the high input wheat systems of northwestern Mexico, where farmers apply an average of 250 kg N/ha, researchers have recorded large N leaching losses (Riley et aI., 2000) and high emissions of greenhouse gases into the atmosphere (Matson et aI., 1998). If cultivars and crop management systems remain as they are now, as N rates increase, the problems of N leaching and greenhouse gas emissions (N_2O), common in many industrialized countries, will also become widespread in the high input areas of developing countries.

Strategy for improving nitrogen use eHiciency

Grain yields of CIMMYT bread wheats developed between 1950 and 1985 have gradually increased. We evaluated these wheats at N levels commonly applied by farmers in irrigated areas of the developing world (75-150 kg N/ha) and found that 50% of the yield gains was associated with higher nitrogen uptake efficiency and the other 50% with better utilization efficiency (Ortiz-Monasterio et aI., 1997a). This cleafly shows that improvements in both uptake and utilization efficiency have been important in the past and most likely will continue to be in the future.

Hence, it is important to select and evaluate for nitrogen use efficiency under both low and high nutrient conditions; this allows the researcher to identify genotypes that perform well under nutrient stress (low input) (efficient) and genotypes that respond well to high input conditions (responder) (Picture 1).

In a study that evaluated five N selection treatments (low, medium, high, alternating high-low, and alternating lowhigh N levels), we found that the highest yielding germplasm in medium or high input environments was obtained by alternately selecting (from F2 to F7) under high and low N conditions. No differences between N selection treatments were observed when the resulting lines were evaluated in low N environments (van Ginkel et aI., 2001).

Picture 1. Varieties with and without nitrogen application, Ciudad Obregon, Sonora, Mexico. (Photo: J.I. Ortiz-Monasterio.)

We conclude that the relative importance of both uptake and utilization efficiency will vary according to the needs of different production systems. Given that wide adaptation is a primary objective in breeding CIMMYT germplasm, we will continue to improve both components.

Phosphorus

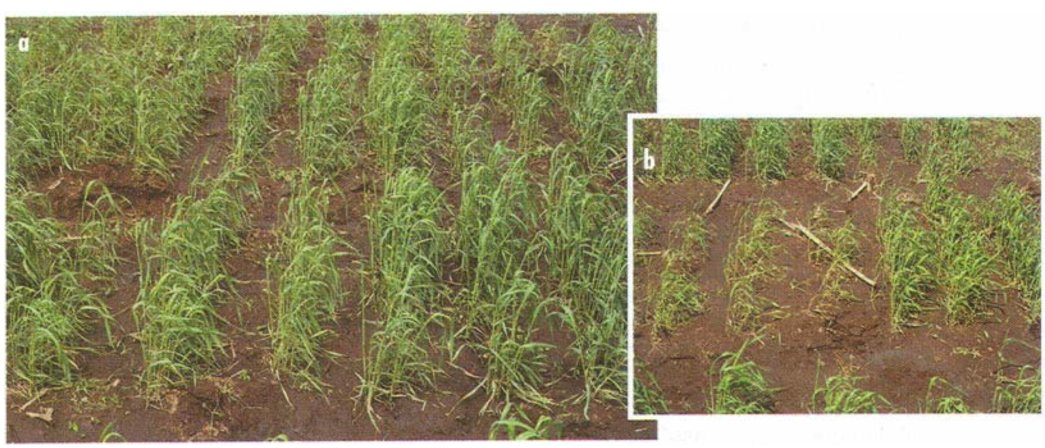
Many soils have large reserves of total phosphorus, but low levels of "available" phosphorus. AI-Abbas and Barber (1964) reported that total soil P is often 100 times higher than the fraction of soil P available to crop plants. Our objective in breeding for P efficient and responsive cultivars has been to identify wheat cultivars that can access P not usually available to the average cultivar under low P conditions (P efficiency), but also respond to P applications (P responsiveness).

As in the case of N, CIMMYT has been breeding under medium to high levels of P in the soil. Preliminary results suggest that phosphorus use efficiency in CIMMYT bread wheatcultivars between 1950 and 1992 has improved under low as well as high levels of P fertility (OrtizMonasterio et aI., unpublished data). Again using Gerloff's (1977) definition, CIMMYT bread wheat germplasm has become more efficient as well as more responsive to P applications during that time period.

There is little information on the contribution of uptake and utilization to total P use efficiency in wheat. In a recent CIMMYT study, the relative importance of uptake and utilization in spring wheat was evaluated in two different environments: a rainfed area with Andisols in the central highlands of Mexico and an irrigated, low-altitude area with Vertisols in northwestern Mexico. Uptake and utilization were characterized in a set of CIMMYT lines. Results showed that in an acid Andisol with no Al toxicity, uptake was more important than utilization in explaining P use efficiency. In contrast, in the same group of genotypes utilization efficiency was more important when evaluated in an alkaline Vertisol (Manske et aI., 2000a). In these two different environments it was shown that there was genetic diversity for both uptake and utilization efficiency in the CIMMYT material tested.

This study shows that, as in the case of N, the environment where a given set of genotypes is evaluated plays a very important role in the expression of P uptake and utilization efficiency. However, in the case of P, what influenced the expression of uptake vs. utilization was not low P vs. high P, but rather the effect of location. At this point it is not clear how much of the location effect is due to soil effects and how much to above-ground effects (radiation, temperature, etc.) (Manske, 1997). Also to be determined is why the same genetic material expresses genetic diversity for uptake efficiency in some environments but not in others.

Evaluating germplasm under both low and high nutrient conditions allows the identification of genotypes that perform well under nutrient stress (low input) and genotyp~s that are responsive to high input conditions (Picture 2). Preliminary data suggest that evaluating advanced



Picture 2. Screening plots for phosphorus use efficiency, Patzcuaro, Michoacan, Mexico. In both pictures, plants on the right received 80 kg P fha, while the ones on the left received none. (a) P use efficient genotype. (b) P use inefficient genotype. (Photos: J.I. Ortiz-Monasterio.)

genetic materials under low P conditions is useful for identifying exceptional germplasm for P stress conditions. When advanced genetic materials are evaluated only under high input conditions, this sometimes results in genotypes that are outstanding under low P conditions, but intermediate under high input conditions. This germplasm might be discarded if it is tested only under high input conditions (since only the top 10-15% of the lines are selected) and its performance under high input conditions is intermediate (Trethowan et aI., unpublished data). Hence the importance of selecting and evaluating under both low and high nutrient conditions. More definite data will be available once a CIMMYT study is completed in which germplasm is selected under low vs. high and under alternating low and high P levels, as was done in the N study.

In acid soils P deficiency is often accompanied by Al and Mn toxicity, especially when soil pH is below 5.4. Evidence available so far indicates that genes controlling adaptation to Al and Mn toxicity and tolerance to P deficiency appear to be independently inherited and recombinable (Polle and Konzak, 1990). Therefore the recommendation is that screening for P use efficiency be done first in soils without Al or Mn toxicity, if possible. Once elite materials have been selected for P use efficiency in the field, they can be screened for Al and/or Mn toxicity either in the field or in hydroponics (see chapter by Hede and Skovmand).

We suggest that screening for P uptake efficiency under nutrient culture conditions be avoided until a satisfactory correlation between performance in the field and in nutrient cultures has been shown. This is particularly important for P, given that very little of the crop's P requirement is provided by mass flow (transpiration flow). Diffusion is more important, but difficult to simulate in solution culture. It is generally recognized that nutrient culture should be limited as a screening environment primarily because of the low correlation of the results with those of field tests. Nutrient cultures cannot simulate the soil-plant interface properly.

Phosphorus uptake vs. utilization eHiciency Phosphorus utilization efficiency (grain yield per unit P in the plant) is dependent on the plant's internal P requirement. Increased harvest index, P harvest index, and low P concentration in grain may improve P utilization efficiency (Jones et aI., 1989; Batten, 1992).

Most CIMMYT high yielding wheats have a P harvest index of about 80% under irrigated conditions. As in the case of N, breeding for higher P utilization efficiency, given the small margin to breed for higher HI, will result in lower P concentration in the grain. Selection for wheat genotypes that remove small amounts of P from the soil due to their low P grain concentration can contribute to sustainable land use (Schulthess et aI., 1997). Genotypic differences in grain P concentration are fairly consistent across environments (Schulthess et al., 1997). If breeders in Australia, which is a major exporter of wheat grain but has soils that are poor in P availability, can reduce the P concentration in the grain of wheat cultivars, farmers will have to purchase substantially less P to replace the P exported with the grain.

However, the strategy of reducing P concentration in the grain has a limit. There is evidence that excessively low values of P concentration in the grain affects seed vigor, particularly in P deficient soils. A study on a set of historically important CIMMYT semidwarf bread wheats showed that P concentration in the grain decreased significantly over the years as a result of breeding (Manske, 1997). Similar information is available from a wheat breeding program in Argentina (Calderini et aI., 1995). As in the case of N, this reduction in P concentration in the grain is associated with gains in utilization efficiency.

Most nitrogen absorbed by plants comes from mass flow (i.e., soil water moves towards the roots as the plant loses water through transpiration), but phosphorus is absorbed mainly by diffusion through gradients created by root absorption. Phosphate concentrations in soil solution are small «0.05 ~ g-l) compared to nitrate-N concentrations (100 ~ g-l), and very little phosphate is moved to the roots by capillary water movement. The amount of P extracted is limited by P concentration at the root-soil interface, which means that wheat roots have to grow to come into contact with new soil from which they can extract phosphate. Root length is thus a major determinant of the absorbing surface area.

Wheat genotypes with greater root length density are able to take up more phosphorus (Manske et aI., 2000b). When P supply is low, the correlation between root length density and P uptake or grain yield is usually 0.50-0.60, but with adequate P supply this correlation is lower. In some environments, P uptake can be more important than utilization efficiency. In areas where uptake is the main component associated with P use efficiency, P uptake efficiency holds great promise for improving P use efficiency, since soils with relatively high levels of total P in the soil often have low levels of available P.

Strategies for improving phosphorus use eHiciency

Different approaches can be used to enhance P uptake (polle and Konzak, 1990; Johansen et aI., 1995).

Increasing the root surface/soil contact area. This can be achieved by modifying root morphology. For a constant level of root biomass, roots with higher specific root length (i.e., roots with smaller diameter) can cover a larger surface area. A second approach for achieving the same objective is through increased hair root development. Root fineness or branching is an important determinant of P uptake efficiency in wheat (Jones et aI. 1989). This route seems promising given that there is evidence of large genetic variability for this trait in wheat. However, the time consuming and labor intensive methodologies currently in use limit its application in breeding programs where large numbers of genotypes need to be screened.

Increasing the effective root area. Root symbiosis with arbuscular mycorrhizal fungi (AMF) has been shown to enhance P absorption by increasing the effective root area (Hayman and Mosse, 1971). AMF infection improves P influx (P uptake per unit root length). On the other hand, the information available discussing the genetic diversity present among wheat cultivars to associate with vesicular-arbuscular mycorrhiza (V AM) is not consistent (Vlek et aI., 1996). There are reports that show differences in mycorrhizal association among wheat cultivars (Vlek et aI. 1996). In contrast, extensive screening of CIMMYT's spring wheat cultivars for mycorrhizal association found very small differences among genotypes; the differences were not strongly associated with higher P absorption (Manske et aI., 2000b).

Increasing nutrient availability through rhizosphere modification. Root exudates, ranging from protons to complex organic molecules, can influence nutrient availability and uptake. Phosphatases have been reported to transform poorly available organic phosphorus, which usually accounts for 40-50% of a plant's total P supply, into inorganic forms available to the plant (Randall, 1995). There are genotypic differences in root phosphatase excreted or bound at the root surface (McLachlan, 1980). Our work in an Andisol showed an association between acid phosphatases and P uptake in different wheat and triticale cultivars (PortillaCruz et aI., 1998).

As in the case of N, most opportunities for breeding for higher utilization efficiency probably lie in improving biomass production efficiency (BPE) rather than HI. In this case biomass production will have to either increase with the current levels of P in the plant or be maintained with a lower concentration of P in the plant. Utilization efficiency is associated with the efficiency with which plants use absorbed P; this, in turn, is a function of 1) how efficiently P is distributed to the functional sites and 2) the P requirement of the cells at those sites (Loneragan, 1978).

Calculating Nutrient Uptake Efficiency

As defined earlier, uptake efficiency refers to the ability of the crop to extract or absorb nutrients from the soil.

Uptake efficiency = Total above-ground nutrient in the plant at maturity (Nt)/Nutrient supplied (Ns)

Uptake efficiency can be measured at any stage of development, but particularly useful information can be collected at anthesis and physiological maturity. Follow the steps described below to measure uptake efficiency.

First, a biomass sample is collected by either harvesting all the above-ground biomass in a given area (a minimum of 0.5 m2 is suggested) or harvesting a predetermined, representative number of plants (a minimum of 50 stems is suggested) at random. Detailed methods for doing this type of sampling at different stages of development are described by Bell and Fischer (1994).

If the sample is collected right before or shortly after anthesis, there is no need to separate the grain from the rest of the plant for N or P analysis. However, if the sample is collected at or around physiological maturity, it is important to separate the grain from the rest of the biomass for N analysis. This is because there is a large difference in % nutrient concentration between the grain and non-grain biomass (leaves, stems, chaff). In well fertilized spring wheat crops under irrigated conditions, we have observed values of approximately 2% N in the grain and 0.8% N in non-grain biomass. Therefore it is best to take a weighted average to calculate total. nutrient in the plant, using the following formula:

Total above-ground nutrient.in the plant at maturity (Nt)
=
[Grain weight at 0% moisture (g m-2) x Nutrient concentration in the grain (%)] +
[Non-grain biomass at 0% moisture (g m-2) x Nutrient concentration in non-grain biomass (%)]

Total nutrient in the plant is then divided by the amount of nutrient supplied (g m-2) as fertilizer. If soil samples are collected and the amount of soil available nutrient is known, this can be added to the amount supplied as fertilizer.

Nutrient absorption is dependent on root characteristics, especially for immobile plant nutrients in the soil, such as phosphorus. Methods for measuring root traits in wheat are explicitly explained in the chapter by Manske et aI.

Calculating Nutrient Utilization Efficiency

Nutrient utilization efficiency is defined as a crop's ability to convert the absorbed nutrients into grain yield.

Utilization efficiency = Tw/Nt

where Tw = total above-ground plant dry weight at maturity and Nt = total above-ground plant nutrient at maturity. To measure uptake efficiency, certain information needs to be collected. First, calculate the harvest index (HI), as follows:

HI = Gw/Tw

where Gw = grain weight at 0% moisture and Tw = total plant biomass at 0% moisture.

This can be done either on an area or a plant basis, as suggested by Bell and Fischer (1994). Finally, biomass produccion efficiency (BPE) is calculated as:

BPE = Gw/Nt

Conclusions

Bread wheat breeding work at CIMMYT has shown that selection and evaluation of genetic material under medium to high nitrogen levels results in genetic gains expressed when this material is tested under low, medium, or high nitrog«p. levels. In other words, selecting for high yield potential under optimum conditions has resulted in germplasm with higher nitrogen use efficiency under low, medium, or high nitrogen fertility conditions. Now there is evidence that breeding under alternating low and high nitrogen levels may produce germplasm that is even more efficient and responsive to nitrogen.

It is clear that nutrient use efficiency and nutrient responsiveness are under genetic control. Some researchers consider these traits as two different breeding objectives, but it has been shown that they are not incompatible. One of the best pieces of evidence for this are the results achieved by bread wheat breeders at CIMMYT. During the last several decades, CIMMYT has been breeding wheat under medium to high levels of nitrogen and phosphorus and has developed cultivars that are not only more responsive to nitrogen and phosphorus, but also more efficient in their use.

To characterize and better understand the mechanisms associated with higher N and P use efficiency:

- Use the definition of Nand P use efficiency suggested by Moll et aI. (1982).
- Distinguish between efficiency and responsiveness. This will require that all germplasm be evaluated under low as well as high Nand P conditions.
- Establish the importance of uptake vs. utilization efficiency in the target environment.
- Understand the mechanisms associated with higher uptake (more roots, phosphatases, etc.) or utilization efficiency (biomass production efficiency vs HI). If these mechanisms are well understood, they can be used as selection criteria.
- Once genetic markers for genes controlling these traits are identified, selection for these traits could be done in the laboratory.

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