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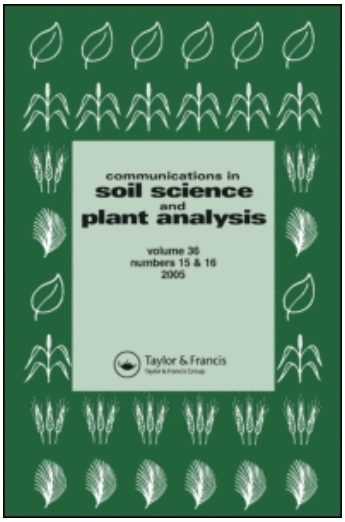

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NUTRIENT USE EFFICIENCY IN PLANTS

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NUTRIENT USE EFFICIENCY IN PLANTS

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ABSTRACT

Invariably, many agricultural soils of the world are deficient in one or more of the essential nutrients needed to support healthy plants. Acidity, alkalinity, salinity, anthropogenic processes, nature of farming, and erosion can lead to soil degradation. Additions of fertilizers and/or amendments are essential for a proper nutrient supply and maximum yields. Estimates of overall efficiency of applied fertilizer have been reported to be about or lower than 50% for N, less than 10% for P, and about 40% for K. Plants that are efficient in absorption and utilization of nutrients greatly enhance the efficiency of applied fertilizers, reducing cost of inputs, and preventing losses of nutrients to ecosystems. Inter- and intra-specific variation for plant growth and mineral nutrient use efficiency (NUE) are known to be under genetic and physiological control and are modified by plant interactions with environmental variables. There is need for breeding programs to focus on developing cultivars with high NUE. Identification of traits such as nutrient absorption, transport, utilization, and mobilization in plant cultivars should greatly enhance fertilizer use efficiency. The development of new cultivars with higher NUE, coupled with best management prac-

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tices (BMPs) will contribute to sustainable agricultural systems that protect and promote soil, water and air quality.

INTRODUCTION

World population is expected to increase from 6.0 billion in 1999 to 8.5 billion by 2025. Such an increase in population growth will intensify pressure on the world's natural resource base (land, water, and air) to achieve higher food production. Increased food production could be achieved by expanding the land area under crops and by increasing yields per unit area through intensive farming. About 1.44 billion ha of the world's land is arable and is under permanent cropping (FAO 1992, 1993). Most of the land that could be brought under cropping has been utilized with exception of some land in Sub-Saharan Africa and South America (Borlaug and Doswell, 1993). Intensive cultivation invariably leads to degradation of land and lowers its fertility and productivity. Many agricultural soils of the World are deficient in one or more of the essential nutrients to support healthy and productive plant growth. Acidity, alkalinity, salinity, erosion, anthropogenic processes and farming practices have contributed to soil degradation and lowering of fertility across different agroecosystems. Mineral stress problems in various soil orders of the world are due to the nature of parent materials and climatic factors (Dudal, 1976). Acidic soils occupy close to four billion ha of the ice-free land area in the world. The total area of salt affected soils in the world is about 950 million ha. Worldwide elemental deficiencies for essential macro and micro nutrients and toxicities by Al, Mn, Fe, S, B, Cu, Mo, Cr, Cl, Na, and Se, have been reported (Table 1; Baligar and Fageria, 1997).

Chemical fertilizers are one of the expensive inputs used by farmers to achieve desired crop yields. Currently, about 12 million tons of N, 2 million tons of P, and 4 million tons of K are being used annually in North American agriculture (Table 2). Recovery of applied inorganic fertilizers by plants is low in many soils. Estimates of overall efficiency of these applied fertilizers have been about 50% or lower for N, less than 10% for P, and close to 40% for K (Baligar and Bennett, 1986, a, and b). These lower efficiencies are due to significant losses of nutrients by leaching, run-off, gaseous emission and fixation by soil. These losses can potentially contribute to degradation of soil, and water quality and eventually lead to overall environmental degradation. These are compelling reasons of the need to increase NUE.

Graham (1984) defined nutrient efficiency of a genotype (for each element separately) as the ability to produce a high yield in a soil that is limited in that element for a standard genotype. More recently Blair (1993) defined nutrient efficiency as the ability of a genotype/cultivar to acquire nutrients from growth medium and/or to incorporate or utilize them in the production of shoot and root

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Table 1. Potential Element Deficiencies and Toxicities Associated with Major Soil Order[a]

Soil Order U. S. Taxonomy	Soil Group FAO	Element	
		Deficiency	Toxicity
Andisols (Andepts)	Andosol	P, Ca, Mg, B, Mo	Al
Ultisols	Acrisol	N, P, Ca, and most other	Al, Mn, Fe
Ultisols/Alfisols	Nitosol	P	Mn
Spodosols (Podsols)	Podsol	N, P, K, Ca, micro nutrients	Al
Oxisols	Ferralsol	P, Ca, Mg, Mo	Al, Mn, Fe
Histosols	Histosol	Si, Cu	
Entisols (psamments)	Arenosol	K, Zn, Fe, Cu, Mn	
Entisols (fluvents)	Fluvisol		Al, Mn, Fe
Mollisols (aqu), inceptisols, entisols, etc. (poorly drained)	Gleysol	Mn	Fe, Mo
Mollisols (borolls)	Chernozem	Zn, Mn, Fe	
Mollisols (ustolls)	Kastanozem	K, P, Mn, Cu, Zn	Na
Mollisols (aridis) (udolls)	Phaeozem		Mo
Mollisols (rendolls) (shallow)	Rendzina	P, Zn, Fe, Mn	
Vertisols	Vertisol	N, P, Fe	S
Aridisols	Xerosol	Mg, K, P, Fe, Zn	Na
Ardisols/arid entisols	Yermosol	Mg, K, P, Fe, Zn, Co, I	Na, Se
Alfisols/ultisols (Albic) (poorly drained)	Planasol	Most nutrients	Al
Alfisols/aridisols/mollisols (natric) (high alkali)	Solonetz	K, N, P, Zn, Cu, Mn, Fe	Na
Aridisols (high salt)	Solonchak		B, Na, Cl

[a] Baligar and Fageria, 1997; Clark, (1982); Dudal, (1976), and personal communications, S.W. Buol (North Carolina State University, Raleigh, NC) and H. Eswaran (USDA, NRCS, Washington, DC).

biomass or utilizable plant material (seed, grain, fruits, forage). Higher NUE by plants could reduce fertilizer input costs, decrease the rate of nutrient losses, and enhance crop yields. Genetic and physiological components of plants have profound effects on their abilities to absorb and utilize nutrients under various environmental and ecological conditions. Genetic, morphological, and physiological plant traits and their interactions with external factors such as soil moisture and temperature, light, best management practices, soil biological, and fertilizer materials need to be more throughly evaluated to improve the NUE in plants.

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Table 2. Average Yield of Important Food Crops (t ha^{-1})[a]

Crop	Africa	America: North/Central	America: South	Asia	Europe	Oceania	World: Average	World: Recorded Maximum Potential
Wheat	1.65	2.46	2.22	2.39	3.09	2.15	2.47	14.50
Barley	1.33	3.17	1.78	1.53	2.77	1.94	2.33	11.40
Maize	1.71	6.50	2.61	3.73	4.87	5.96	3.79	22.20
Rice	2.21	5.83	3.11	3.80	5.17	6.59	3.73	—
Sorghum	0.86	3.79	3.02	1.18	3.47	2.38	1.46	21.50
Soybean	0.65	2.53	2.17	1.33	1.72	2.28	2.08	5.60
Common bean	0.71	0.92	0.62	0.62	1.11	0.71	0.68	—
Potato	12.07	34.41	12.59	14.42	16.18	28.79	15.47	95.00

[a]Baligar and Fageria, (1997) and FAO, 1997 year book.

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Best management practices are the best external alternative that can be applied to improve NUE. Plant genetics and physiological mechanisms and their interaction with BMPs are also a tool that can be used to increase efficiency of cropping systems. Our objective is to present a broad spectrum of NUE in plants. Several other authors have reported extensively on this topic (Baligar and Duncan, 1990; Baligar and Fageria, 1997; Barber, 1995; Blair, 1993; Duncan, 1994, Duncan and Carrow, 1999; Epstein,1972; Fageria, 1992; Fageria et al., 1997a; Gerloff and Gabelman, 1983; Marschner, 1995; Mengal and Kirkby, 1982; and Vose, 1987).

Estimation of NUE in Plants

The evaluation of NUE is useful to differentiate plant species, genotypes and cultivars for their ability to absorb and utilize nutrients for maximum yields. The NUE is based on (a) uptake efficiency (acquire from soil, influx rate into roots, influx kinetics, radial transport in roots are based on root parameters per weight or length and uptake is also related to the amounts of the particular nutrient applied or present in soil), (b) incorporation efficiency (transports to shoot and leaves are based on shoot parameters) and (c) utilization efficiency (based on remobilization, whole plant i.e. root and shoot parameters).

Some of the commonly used efficiency definitions are given below. For the extensive coverage of this area, readers are referred to Baligar and Duncan (1990); Baligar and Fageria (1997); Blair (1993); Fageria (1992); and Gerloff and Gablemen (1983).

Nutrient efficiency ratio (NER) was suggested by Gerloff and Gabelman (1983) to differentiate genotypes into efficient and inefficient nutrient utilizers.

$$\text{NER} = \frac{(\text{Units of Yields, kgs})}{(\text{Unit of elements in tissue, kg})} \ \text{kg kg}^{-1} \qquad [1]$$

Physiological efficiency (PE) is defined as

$$\text{PE} = \frac{(\text{Yield F kg} - \text{Yield C, kg})}{(\text{Nutrient uptake F, kg} - \text{Nutrient uptake C, kg})} = \text{kg kg}^{-1} \qquad [2]$$

Where F is plants receiving fertilizer and C is plants receiving no fertilizer.

Agronomic efficiency (AE) is expressed as the additional amount of economic yield per unit nutrient applied:

$$\text{AE} = \frac{(\text{Yield F, kg} - \text{Yield C, kg})}{(\text{Quantity of nutrient applied, kg})} = \text{kg kg}^{-1} \qquad [3]$$

Agrophysiological efficiency (APE) has been defined as the economic yield (ex. grain) obtained per unit of nutrient absorbed:

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$$\text{APE} = \frac{(\text{Yield F, kg} - \text{Yield C, kg})}{\underset{\text{Straw + Grain}}{(\text{Nutrient uptake F, kg})} - \underset{\text{Straw + Grain}}{(\text{Nutrient uptake C, kg})}} = \text{kg kg}^{-1} \quad [4]$$

Apparent nutrient recovery efficiency (ANR) has been used to reflect plant ability to acquire applied nutrient from soil:

$$\text{ANR} = \frac{(\text{Nutrient uptake F, kg} - \text{Nutrient uptake C, Kg})}{(\text{Quantity of nutrient applied, kg})} \times 100 = \% \quad [5]$$

ENHANCEMENT OF NUE IN PLANTS

Overall NUE in plant is a funtion of capacity of soil to supply adequate levels of nutrients, and ability of plant to acquire, transport in roots and shoot and to remobilize to other parts of the plant. Plants interaction with environmental factors such as solar radiation, rainfall, temperature and their response to diseases, insects and allelophathy and root microbes have a great influence on NUE in plants. Detailed discussion on these various areas are given in reviews by Baligar and Duncan (1990); Baligar and Fageria (1997); Blair (1993); Duncan (1994); Epstein (1972); Fageria (1992); Fageria et al (1997a); Gerloff and Gabelman (1983); Marschner (1995); and Mengal and Kirkby (1982); and therefore an attempt will be made here to present only the overview of this issue.

Soil Factors

Production potential of many soils in the world are affected by the low supply of nutrients due to adverse soil physical and chemical constraints (Baligar and Duncan, 1990; Baligar and Fageria, 1997; Dudal, 1976; Fageria, 1992; Fageria and Baligar,1997b; Fageria et al., 1997a and b; Foy 1984). In tropical regions the main soil problems in rain fed systems that affect crop production are low soil fertility, salinity, alkalinity, acidity, and Fe toxicity, and P and Zn deficiencies (Baligar and Fageria, 1997; Fischer 1998). Fertilizer efficiency in these soils is profoundly influenced by fertilizer placement and timing (Baligar and Bennett, 1986a, and b; De Datta, 1986). Salinity, acidity, elemental deficiencies, and toxicities, and low organic matter content are some of the major chemical constraints. Physical constrains such as high bulk density layers or pans, poor structure and texture, surface sealing and crusting, high or low water holding capacity, water logging and extreme drying or poor aeration can also reduce NUE. Among other nutrient dynamics, these factors can affect mineralization and immobilization, fixation by adsorption and precipitation mechanisms, leaching, runoff, and gaseous losses via denitrification and ammonia volatilization (Baligar and Bennett, 1986a, and b; Baligar and Fageria, 1997).

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Adverse soil physical properties affect the longitudinal and radial root growth, root distribution, morphology by stunting, thickening, reduction of second and third order lateral roots and root anatomical changes (Bennie, 1996; Russell,1977; Taylor et al., 1972). High mechanical impedance leads to loss of root caps and reduction in radial thickening primarily due to shorter and wider cells with the same volume in the cortex (Camp and Lund, 1964) and a thicker cortex (Baligar et al., 1975). This may also cause changes in cell structure of the endodermis and pericycle (Baligar et al., 1975; Bennie, 1996). Such changes in the size and internal and external morphology of roots due to the adverse soil physical conditions will influence the root's ability to explore larger soil volume and reduce nutrient and water availability and uptake, leading to low NUE and lower yields.

Leaching and crop removal of basic cations, N_2 fixation by legumes, use of heavy levels of organic and inorganic N fertilizers, and atmospheric deposition of N and sulfur oxides are major factors for soil acidification that leads to degradation and lower productivity and soil quality in temperate and tropical regions of the world (Baligar and Ahlrich, 1998; Baligar et al., 1998a; Dudal, 1976; Sumner et al., 1991). Acidic soils have phyto-toxic levels of Al, Mn, Fe, and H and deficient levels of N, P, K, Ca, Mg, Mo, and Zn to support good plant growth (Baligar and Fageria, 1997; Fageria et al., 1990; Sumner et al., 1991). Both of these factors are largely responsible for reduced growth and lower NUE (Baligar and Fageria, 1997; Fageria et al., 1990; Foy,1992; Marschner, 1995 Sumner et al., 1991).

Excess salt affects N uptake by plants and also contributes to reduced permeability of roots, consequently decreasing water and nutrient uptake (Frota and Tucker, 1978). Francois et al. (1988) reported that in triticale, increasing salinity reduced plant concentrations of Ca, Mg, and P significantly, but had no effect on the Na, K, and Cl concentrations. Gupta and Abrol (1990) reported that it is common to find toxic concentrations of Na, Mo, B, Se and bicarbonates in salt affected soils. Saline soils contain predominantly chlorides and SO_4^{-2} of Na, Ca, and Mg while alkaline soils contain excess levels of $NaHCO_3$ and exchangeable Na (Baligar and Duncan, 1990; Baligar et at., 1998a; Barber, 1995; Fageria, 1992; Fageria et al., 1997a; Marschner, 1995).

During recent decades the soil concentrations of elements such as Cd, Cr, Ni, Pb, Cu, Zn, As, Co, and Mn in some agricultural soils have been increasing due to use of soil amendments, pesticides and other anthropogenic activities (Adriano ,1986; Alloway, 1995; Kabata-Pendias and Pendias, 1992). These trace elements, if present at excess levels pose phyto-toxicity and can reduce plant growth and nutrient uptake and eventually reduce NUE (Baligar et al., 1998a; Kabata-Pendias and Pendias, 1992; Marschner, 1995). The availability of these heavy metals will be affected by soil pH, temperature, redox potentials, anion ligand formation, and composition and quantity of soil solution among other factors (Alloway 1995).

Root morphology parameters such as length, thickness, surface areas, density, root hairs and root growth rate expressed as dry mass and/or root: shoot ratios

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are affected by deficiencies of essential minerals and/or excess of minerals (Baligar et al., 1998a; Bennet, 1993; Hagemeyer and Breckle, 1996; Fageria et al., 1997a, and b; Foy, 1992; Kafkafi and Bernstein,1996; Marschner, 1995). Clark (1970) reported that in solution culture studies with maize, reducing the supply of essential nutrients from full strength to none increased root: shoot ratio in P, Ca, S, and Zn treatments; however, root: shoot ratios decreased in NO_3-N, Mg, Mn, and Cu treatments.

Effects of soil organic matter (SOM) on physical parameters and nutrient dynamics and how they impact NUE have been reported by several authors (Baligar and Fageria, 1997; Fageria, 1992; von Uexkull, 1986). The SOM helps to maintain good aggregation and increase water holding capacity and exchangeable K, Ca, and Mg. It also reduces P fixation, leaching of nutrients and decreases toxicities of Al and Mn. Best management practices such as addition of crop residues, green manure, compost, animal manure, use of cover crops, reduced tillage and avoiding burning of crop residues can significantly improve the level of SOM and contribute to the sustainability of the cropping systems and higher NUE.

Liming is an effective way to correct soil chemical constraints (Adams, 1984) . It improves the availability of Ca, Mg, Mo, P, soil structure, and CEC. The fixation of atmospheric dinitrogen (N_2) by free living and symbiosis organisms like *rhizobium* is increased. Potential toxicity of Al and Mn is reduced (von Uexkull, 1986). Lime has very low mobility in soil and when surface applied it does not reduce the acidity of sub-surface soil horizons. Contrary to lime, gypsum ($CaSO_4$) has a greater downward movement and when applied to the surface it can still impact and reduce the acidity of the subsoil (Farina and Channon, 1988; Ritchey et al., 1980). Downward movement of Ca in soil has resulted in increased rooting depth and in higher uptake rates of N, Ca, Cu, P and Mn by corn (*Zea mays L*) grown in Cerrado acid Oxisol of Brazil (Sousa et al., 1992). Reduction of subsoil acidity usually leads to deeper rooting and higher water and mineral uptake by plants (Baligar and Fageria, 1997; Fageria, 1992; Fageria et al., 1995).

About half of the world's soils are deficient in micronutrients. If new cultivars that have higher yields are developed, the dynamics of micronutrient could change due to larger removal of these elements from the cropping systems in the harvested portions of the crops. In such a case, micronutirents will have to also be monitored for these soils to ensure that higher yields and NUE are maintained.

Fertilizer Factors

The fertilizer use efficiency is affected by several factors such as soil properties, efficiency of crops, climate, chemical species of the fertilizer used (eg urea, NH_4^+-N or NO_3^--N), mycorhiza, and others (Baligar and Bennett, 1986a and b; Fageria, 1992; Hauck 1985). The availability and recovery efficiencies of fertiliz-

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ers, are greatly affected by amendments such as lime, organic materials and others, due to their effects in nutrient dynamics (Adams, 1984; Baligar et al., 1998a; Baligar and Duncan, 1990; Fageria et al., 1997b; Stevenson, 1986; von Uexkull, 1986). Best management practices such as source, rate, method of application, and split application of nutrients should be optimized based on soil, plant, and climatic factors to reduce nutrient losses due to leaching, denitrification, ammonia volatilization, runoff, and fixation. Several authors have reported this improvement and careful considerations to these several factors increases NUE of added fertilizers (Engelstad, 1985; Khasawneh et al.,1980; Motrvedt et al., 1991; Munson, 1985; Peoples et al., 1995; Stevenson, 1982).

Changes in the soil nutrient reserve and alteration in root systems under different tillage systems might have direct bearing on the nutrient availability and uptake by crops. Tillage practices such as conventional, conservation and no-tillage are known to bring changes in SOM, nutrient concentrations, bulk density, water holding capacity and soil temperature among others. Higher contents of available P, Ca, K and organic C and N have been reported for no tillage than for conventional tillage (Blevins et al., 1983; Ismail et al., 1994; Lal, 1976; Mahboubi et al., 1993; Saffigna et al.,1989). Minimum tillage increases root growth in the top 12 cm of soil for barley (*Hordeum vulgare L*) and oat (*Avena sativa L*) cropping systems (Ehlers et al., 1983: Ellis et al., 1977). Minimum tillage has also been reported to increase root weight, length, and density, increasing the nutrient and water use efficiencies (Adkinson,1990; Hackett,1969; Mengal and Barber, 1974). Baligar et al., (1998b) reported that shoot dry matter yields and root length and density of silage corn in no-till were significantly higher than in conventional tillage. Such improved root parameters contributed to higher yields and uptake efficiencies of N., P, Ca, S, Cu, Fe, and Zn. Improved tillage equipment and practices need to continue being developed to increase NUE across different agroecosystems.

Slow and controlled release fertilizers have added advantages in increasing nutrient recovery by plants, lowering N_2O and NH_3 emissions and NO_3^--N leaching from cropping systems, while suppling a lasting nutrient source (Delgado and Mosier 1996, Hauck, 1985; Peoples et al., 1995; Prasad and Power, 1995). Slow release N fertilizers such as Meister (Chisso-Assahi Fertilizer Corp), CDU and IBDU (Mitsubishi chemical industries) are currently in the market (Hauck, 1985; Peoples et al., 1995; Prasad and Power, 1995). There is the need for additional research with these slow and controlled release fertilizers and their interaction with different management situations, soil types and cropping systems.

Nitrification inhibitors that are widely used are N-serve [2-chloro-6 (trichloromethyl) pyridine], AM [2-amino-4chloro 6 methylpyrimidine], DCD (Dicyandiamide), and KN3 (Hauck, 1985; Peoples et al., 1995; Prasad and Power, 1995). Application of neem cake, PPD (phenly phosphorodiamidate), and NBPT [N-(n-butyl) thiophosphoric triamide] with urea has been suggested to reduce the rate of

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urea hydrolysis and improve its efficiency (Hendrickson, 1992; Peoples et al., 1995; Prasad and Power, 1995). Nitrificator inhibitors such as DCD have the potential to reduce N_2O emissions and increase NUE of irrigated systems such as barley (Delgado and Mosier, 1996). Research and development is needed to continue developing new procducts that can increase the recovery of fertilizers while maintaining and or increasing yields and protecting the environment.

Site specific (precision) technology in the future might help to develop sound management systems and lead to reduced fertilizer inputs, thereby improving costs of fertilizer input and the degradation of the environment. The UN–FAO has suggested the integrated plant nutrition system (IPNS) with the objective of maintenance and possible improvement of soil fertility for sustainable crop productivity (Baligar and Fageria, 1997). Fageria and Baligar (1997b) have suggested the Integrated Plant Nutrient Management System (IPNMS). The IPNMS has been defined as the package of practices for the manipulation of the plant growth environment to supply essential nutrients to a crop in an adequate amount and proportion for optimum production without degrading the natural resources.

Plant Factors

Selection of improved genotypes adaptable to a wide range of climatic changes has been a major contributor to the overall gain in crop productivity. Steady increase in the average yields of major crops during the second half of the 20th century has been achieved through genetic improvement coupled with improvement in best management practices. In spite of such advances, the average production of major crops at the farm level, are still two to four times lower than the recorded maximum potentials (Table 2). Modern genotypes of rice (*Oriza sativa L*), corn, wheat (*Triticum aestivum L*) and soybean (*Glycine max L. Merrill*) are more efficient in absorption and utilization of nutrients as compared to older cultivars (Clark and Duncan, 1991; Fageria, 1992). Borlaug and Doswell (1994) stated that soil fertility is the single most important factor that limits crop yields in developing countries. As much as 50% of the increase in crop yields worldwide during the 20th century is due to the use of chemical fertilizers.

High crop yields in North America, Europe, and Asia could be correlated to high use of nutrients (Table 3). In spite of high fertilizer use the average yields in Asia are still lower than North America mainly due to lower efficiency of applied fertilizers, use of low yielding cultivars and occurrence of drought. Some of the highest gain in fertilizer use in Asia has been in East and South Asia, where dramatic increases in crop yields have been achieved. Lower crop yields in Africa and South America might have been caused by lower soil productivity, and lower use of fertilizers and amendments. Climatic stress such as water deficits and the low availability of seeds of improved cultivars are also affecting cropping systems

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Table 3. Nutrient Use (10^6 Tons) and Average Regional NPK Fertilizer Use (kg/ha) in Different Regions of the World

Parameter	Africa	America North/ Central	America South	Asia	Europe	Oceania	World
Nutrient Use[a]							
N	2.13	12.62	2.42	44.87	14.47	0.81	78.74
P	0.43	2.06	0.94	7.16	2.15	0.55	13.55
K	0.38	4.33	1.67	5.73	4.85	0.30	17.52
Regional N-P_2O_5-K_2O Use[b]	19.00	92.00	66.00	129.00	134.00	44.00	85.00

[a] Data for 1995–1996 personal communication B.L. Bumb IFDC. Muscle Shoals, AL, Bumb (1995).
[b] Based on FAO, 1996a, b and personal communication. B. L. Bumb IFDC Muscle Shoals, AL.

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of Africa and South America. The implementation of best management practices that use the plant genetic components, climatic variables, and timely supply of water, nutrients and control of pests and weeds will be needed to maximize potential yield production for these regions.

Genetic variability has been reported to explain the differences in NUE and the parameters of nutrient uptake (Baligar and Duncan, 1990; Baligar and Fageria, 1997; Barber, 1995; Clark,1982; Clark and Duncan, 1991; Duncan, 1994; Duncan and Carrow, 1999; Epstein, 1972; Foy, 1983; Gerloff, 1987; Gerloff and Gabelman, 1983; Vose, 1984). Such differences in growth and NUE in plants have been related to differences in absorption, translocation, shoot demand, dry matter production per unit of nutrient absorbed, and environmental interactions (Baligar and Duncan, 1990; Clark, 1982 and 1984; Clark and Duncan, 1991; Gerloff and Gabelman, 1983; Vose, 1984). Overall NUE in plants is governed by the flux of ions from the soil to the root surface and by the influx of ions into roots followed by their transport to the shoots and remobilization to plant organs. Various soil and plant mechanisms and processes that contribute to such differences are given in Table 4, for in-depth review see Baligar and Duncan (1990), Baligar and Fageria (1997), Barber (1995), Epstein, (1972), Gerloff, (1987), Lauchli and Beleski, (1983a and b).

The root morphological factors such as length, thickness, surface area, and volume have profound effects on the plant's ability to acquire and absorb nutrients in soil (Baligar and Duncan, 1990; Barber, 1995). These parameters influence the ability of the roots to penetrate high density soil layers, to tolerate temperature and moisture extremes, and toxicities and deficiencies of elements. Additionally, the ability to modify the rhizosphere pH, and the nutrient uptake kinetics are also affected by root morphology. The physiological and biochemical parameters and their interaction with external factors affect NUE (Table 5; Baligar and Bennett, 1986a and b; Baligar and Fageria, 1997; Duncan,1994; Peoples et al., 1995; Munson, 1985; Khasawneh et al., 1980). Sauerbeck and Helal, (1990) summarized root activities that affect nutrient availability in the rhizosphere as follows: (a) modification of rhizosphere pH; (b) exudation of organic acids, chelators, reductants, and oxidants; (c) extracellular enzymes to turn over organically bound nutrients; and (d) providing substrate for microbial biomass.

External factors such as soil management, climatic factors, allelopathy, diseases, and weeds profoundly affect the plants ability to absorb and utilize nutrients more effectively (Baligar and Bennett 1986a and b; Baligar and Fageria, 1997; Fageria, 1992; Fageria et al., 1990 and 1997a). Soil temperature and moisture greatly influence nutrient transformation (release) from organic forms, their uptake by roots and their subsequent translocation and utilization by plants. Plant health is influenced by diseases, insects and weeds that compete for nutrients and water resources and lower NUE. For extensive coverage of these areas see

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Table 4. Soil and Plant Mechanisms and Processes and Other Factors That Influence Genotypic Differences in Nutrient Efficiency in Plants Grown Under Nutrient Stress Conditions[a]

A. Nutrient acquisition
   1. Diffusion and mass flow (buffer capacity, ionic concentration, ionic properties, tortuosity, soil moisture, bulk density, temperature)
   2. Root morphological factors (number, length, root hair density, root extension, root density)
   3. Physiological [root:shoot, root microorganisms such as mycorrhizal fungi, nutrient status, water uptake, nutrient influx and efflux, rate of nutrient transport in roots and shoots, affinity to uptake (Km), threshold concentration Cmin]
   4. Biochemical (enzyme secretion as phosphatase, chelating compounds, phytosiderophore), proton exudate, organic acid production such as citric, trans-aconitic, malic acid exudates

B. Nutrient movement in root
   1. Transfer across endodermis and transport within root
   2. Compartmentalization/binding within roots
   3. Rate of nutrient release to xylem

C. Nutrient accumulation and remobilization in shoot
   1. Demand at cellular level and storage in vacuoles
   2. Retransport from older to younger leaves and from vegetative to reproductive parts
   3. Rate of chelates in xylem transport

D. Nutrient utilization and growth
   1. Metabolism at reduced tissue concentration of nutrient
   2. Lower element concentration in supporting structure, particularly the stem
   3. Elemental substitution, e.g. Na for K function
   4. Biochemical (nitrate reductase for N-use efficiency, glutamate dehydrogenase for N metabolism, peroxidase for Fe efficiency, pyruvate kinase for K deficiency, metallothionein for metal toxicities)

E. Other factors
   1. Soil factors
      a. Soil solution (ionic equilibria, solubility precipitation, competing ions, organic ions, pH, phytotoxic ions)
      b. Physico-chemical properties of soil (organic matter, pH, aeration, structure, texture, compaction, soil moisture)
   2. Environmental effects
      a. Intensity and quality of light (solar radiation)
      b. Temperature
      c. Moisture (rainfall, humidity, drought)
   3. Plant diseases, insects, and allelopathy

[a]Baligar and Fageria, (1997); Baligar et al., (1990a); Duncan and Baligar, (1990); Fageria, (1992); Gerloff, (1987).

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Table 5. Plant and External Factors That Affect Nutrient Use Efficiency in Plants

Plant Factors	External Factors
Genetic control	Fertilizers
- Species/cultivar/genotypes	- Source
Physiological	- Ammonification, nitrification inhibitors
- Roots: length, and density of main, lateral and root hair	- Time depth method of placement and application
- Higher shoot yield, harvest index internal demand	- Applying in combination
- Higher physiological efficiency	- Reduce losses (NH_3, NO_3)
- Higher nutrient uptake and utilization	- Use slow release form
Biochemical	Climatic
- Enzymes: nitrate reductase (N), phosphatase (P), pyruvate kinase (K), arginine residue (N), phytic phosphate (P) rhodotorubic acid (Fe)	- Adequate soil moisture
- Proline, aspharagine pinitol (salinity)	- Extreme temperature
- Abscisic acid, proline (drought)	Elements
- Matallothionein (trace element)	- Toxicities: acidic soil (Al, Mn, pH), saline (Na, Mg, Cl, SO_4) and alkaline (Na, Na_2, CO_3) soils
- Root exudate (citric, malic, transaccionitic acid)	- Deficiencies (N, P, K micro)
	Others
	- Arbuscular mycorrhizae, beneficial soil microbes
	- Control of weeds, diseases and insects
	- Incorporate crop residue, cover crops, crop rotation

Baligar and Bennett, (1986a,b) Baligar and Fageria, (1997), Duncan, (1994), Fageria, (1992).

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Baligar and Duncan 1990, Barber 1995, Fageria 1992, Fageria et al., 1997a and Marschner 1995.

In plant uptake and utilization, efficiency of nutrients are governed by different physiological mechanisms (Table 4) and their response to deficiency, tolerance and toxicity of element(s) and climatic variables (Baligar and Duncan, 1990; Baligar and Fageria, 1997; Baligar et al., 1990a; Duncan and Carrow 1999; Gerloff, 1987). Genetic improvement in tolerance to toxicities of Al, Mn, H, Na, trace elements, and salts; and to deficiencies of nutrients, drought, temperature extremes, aeration and high soil bulk density, will enhance the plants' ability to absorb and utilize nutrients more effectively (Arkin and Taylor, 1981; Baligar and Fageria, 1997; Cooper, 1973; Duncan and Carrow, 1999; Graham, 1984; Foy, 1984). The numerous nutritional differences among cultivars and strains of plants indicate genetic control of inorganic plant nutrition (Baligar and Duncan, 1990; Clark and Duncan, 1991; Duncan and Carrow, 1999; Gerloff and Gablemen, 1983; Graham, 1984). Genetic variation for NUE has been widely reported within and among crop species. Gene factors and inheritance of traits related to NUE have been well documented (Clark and Duncan, 1991; Sattelmacher et al., 1994; Duncan and Carrow 1999).

The existence of considerable genotypic variations, techniques and selection criterion could enhance the feasibility of breeding crop cultivars for improved mineral nutrient use efficiency (Fageria and Baligar, 1994; Graham, 1984). Identification of cultivars with greater tolerance to suboptimal soil nutrient levels offer considerable promise for increasing the crop production potential of marginal low fertility lands throughout the world (Baligar and Fageria, 1997; Clark and Duncan, 1991; Duncan and Carrow,1999; Fageria, 1992, Fageria et al., 1997a). When nutrient supply from soil is suboptimal (eg. Acid and salt affected soils), the efficiency with which mineral nutrients are used by plants is important in overall nutrient efficiency. Breeding programs should consider plant characteristics such as the ability to produce near maximum yields at low nutrient levels, and extensive root systems efficient in exploring large soil volumes to produce cultivars with high NUE that can contribute to sustainability and environmental protection (Clark and Duncan, 1991; Sattelmacher et al., 1994; Vose, 1984 and 1987).

Breeding cultivars for high tolerance to low levels of nutrients supply and biotic and abiotic constraints will have a better chance of improving NUE. The potential for breeding improved cultivars with superior NUE largely depends upon: (i) the genetic variability present in the species/cultivar for that particular trait(s) that govern NUE and, (ii) development of methodology to accurately quantify the physiological parameters that reflect efficient NUE (Duncan and Baligar, 1990; Duncan and Carrow, 1999; Fageria and Baligar, 1994; Gerloff, 1987; Gerloff and Gableman, 1983; Vose, 1984, and 1987). Identification of heritable traits (physiological, and biochemical) that relate to the NUE of grain yields or productivity in general appears to be the most formidable barrier for genetic improve-

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ment of plants for high NUE. Conventional plant breeding has enhanced N use efficiency in rice cultivars (Fischer 1998 data from S. Peng) but new methods are needed that can advance how specific traits are identified and pass from one cultivar to the other or from one species to another.

Duncan and Carrow, (1999) and Graham, (1984) state that for N, P, and K, genetic control is generally complex (polygenic) but in many cases appears to be relatively simple or monogenic for micronutrient use efficiencies. Because of the complexity of plant genomes and their impact on ecological, physiological, and biochemical processes in plants, the exact role of genes in NUE is speculative at this time (Duncan, 1994). From the current understanding, more than one mechanism is apparently operating in plants to control uptake, transport and utilization of nutrients (Barber, 1995; Duncan and Carrow, 1999; Epstein, 1972; Marschner, 1995; Welch 1995). It is unclear whether the control of ion uptake is in the roots, or shoots or both. Water demand and absorption through roots and its upward translocation to shoot, together with the downward translocation of photosynthates and hormones are probably driving forces in overall nutrient uptake and utilization efficiency, but its unclear at this point how genes responsible for these processes interact for higher NUE.

Most efficient (E) and most inefficient (I) nutrient efficiency ratios (NER) in different species and cultivars/genotypes within species have been reported (Baligar and Duncan, 1990; Baligar et al., 1987, 1989a and b, 1990a and b, and 1997; Clark, 1984; Clark and Duncan, 1991; Fageria and Baligar, 1997a, and 1999; Fageria et al., 1988a and b; Gerloff and Gabelman, 1983). Table 6 lists NER for P, K, Ca, and Mg in selected species of plants. Overall efficient entries were far superior in utilization of absorbed nutrients than the inefficient entries. Different NUE parameters for N, P, and K in rice genotypes grown in lowland acid soils of Brazil are presented in Table 7. With a few exceptions genotype CNA 571 was far superior in uptake, utilization and apparent recovery of N, P, and K than inefficient genotype CNA 5804. Such an evaluation will help to identify superior genotypes that could be incorporated into breeding programs to produce desirable cultivars.

Levels of fertilizer applications influence the total dry matter accumulation thereby affecting the nutrient demand (uptake/utilization). Increasing applications of N from 0 to 210 kg ha^{-1} reduces overall N use efficiency in low land rice (Table 8). In this study the apparent recovery efficiency of N at 210 kg ha^{-1} was 32%. Such low N recoveries may be related to N losses from soil via denitrification, ammonia volatilization, and NO_3^--N leaching (Craswell and Vlek, 1979).

Fageria and Baligar (1994) have grouped genotypes into four classes based on grain yield response index (GI; Eq. 6). They used the GI to group corn and wheat genotypes into four P responsive groups (Fageria and Baligar, 1997a, and 1999). The genotypes were grouped as (a) non-efficient and non-response (NENR), (b) non-efficient and responsive (NER), (c) efficient and responsive (ER), and (d) ef-

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Table 6. Variations in Nutrient Efficiency Ratio (NER) Values for P, K, Ca, and Mg of Most Efficient (E) and Inefficient (I) Entries of Selected Crop Species

		NER[a]			
Species	Efficiency	P	K	Ca	Mg
Bean[b]	E	671	294	—	—
	I	562	154	—	—
Red clover[c]	E	1012	104	91	670
	I	470	61	53	476
Tomato[b]	E	—	357	434	—
	I	—	173	381	—
Maize[d]	E	625	46	256	476
	I	171	18	115	333
Sorghum[e]	E	1000	44	208	417
	I	476	23	123	278
Wheat[f]	E	188	—	—	—
	I	125	—	—	—
Rice[g]	E	1125	—	—	—
	I	563	—	—	—
Alfalfa[h]	E	629	78	102	1091
	I	403	48	58	734

[a]NER = mgs of shoot weight mg^{-1} element in shoot.
[b]Gerloff and Gabelman, (1983).
[c]Baligar et al., (1987).
[d]Baligar et al., (1997).
[e]Baligar et al., (1989a).
[f]Fageria and Baligar, (1999).
[g]Fageria et al., (1988a).
[h]Baligar et al., (1990 b).

ficient and nonresponsive (ENR). Genotypes falling into the ER group would be most desirable because they can produce high yields at low as well as high levels of nutrient availability. Cultivars in the ENR group would also be desirable because they produce high yields at low nutrient availability.

$$\mathrm{GI} = \frac{(\text{Yield in non P stress soil}) - (\text{Yield in P stress soil})}{(\text{Differences in applied P levels between non-stress and stress})} = \mathrm{kg\ kg^{-1}} \quad [6]$$

Gerloff (1977) and Blair (1993) differentiated plants into four classes based on plant response to available nutrients. Efficient responder-plants were those that produce high yields at low levels of nutrients and that respond to higher levels of

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Table 7. Nutrient Use Efficiency[a] for N, P, and K of Lowland Rice Genotypes Grown in Acid Soil of Central Brazil[b]

Elements	Genotypes	Nutrient Efficiency Ratio	Physiological Efficiency	Agronomic Efficiency	Agro-physiological Efficiency	Apparent Recovery Efficiency
		kg kg^{-1}				%
N	CNA571	98	141	42	60	70
	CNA6804	65	261	35	167	30
P	CNA571	172	533	79	226	33
	CNA5804	115	363	67	234	33
K	CNA571	68	119	64	51	58
	CNA5804	45	89	54	58	51

[a] For definitions for various NUE parameters refers to Equations 1 to 5 in the text.
[b] Fageria unpublished.

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Table 8. Nitrogen Use Efficiencies[a] Under Different N Rates Across Three Years[b]

N Rate kg ha^{-1}	Nutrient Efficiency Ratio	Physiological Efficiency	Agronomic Efficiency	Agro-physiological Efficiency	Apparent Recovery Efficiency %
	kg kg^{-1}				
30	76	156	35	72	49
60	83	166	32	73	50
90	67	182	22	75	37
120	50	132	22	66	38
150	50	146	18	57	34
180	42	126	16	51	33
210	36	113	13	46	32
Average	58	146	23	63	39
Regression Coefficient					
B_0	89.00	180.86	37.12	82.86	57.57
B_1	−0.26	−0.29	−0.12	−0.17	−0.10
R^2	0.90**	0.62^{NS}	0.93*	0.87*	0.82*

[a]For definition of various NUE refer to equations 1 to 5 in the text.
[b]Fageria unpublished.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

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nutrient additions. Inefficient responder-plants were those with low yields at low levels of nutrition that have a high response to added nutrients. Efficient non-responder-plants produce high yields at low levels of nutrition but do not respond to nutrient additions. Inefficient-responder-plants produce low yields at low levels of nutrition and do not respond to nutrient addition.

Agronomic Consideration

Minimum tillage, no tillage, conservation tillage and traditional tillage can bring profound changes in soil quality, SOM and nutrients throughout different soil horizons (Blevins et al.,1983; Lal, 1976; Mahboubi et al.,1993). Rooting pattern, water holding capacity, water penetration, aeration, soil compaction, and soil temperature are also influenced by type of tillage practices (Arkin and Taylor 1981). Crop rotation and use of cover crops and green manure crops are known to improve soil fertility and physical properties and to minimize pest and weed problems (Delgado, 1998; Delgado et al., 1999; Fageria, 1992; Fageria et al., 1997a). Improved tillage practices and tillage equipment need to be developed to enhanced NUE in crop plants.

Biological Consideration

Enhanced beneficial microbes such as rhizobia, diazotrophic bacteria, and mycorrhizae in the rhizosphere have improved root growth by fixing atmosphere N_2, suppressing pathogens, producing phytohormones, enhancing root surface area to facilitate uptake of less mobile nutrients such as P and micronutrients, and mobilization and solubilization of unavailable organic/inorganic nutrients. Fixation of N_2 by *Rhizobium* is very effective in humid and sub-humid regions and the reported N_2 fixed ranges from 24 to 267 kg $ha^{-1}y^{-1}$ (Fageria 1992). The amount of N_2 fixed varies, depending on crop species/cultivars, soil acidity, temperature, drainage, and the timing of harvest (Fageria 1992). Ladha et al., (1996) reported that free-living and/or associated phototrophs and heterotrophs in irrigated rice paddies can fix from 50 to 100 kg N ha^{-1}, contributing to the increased supply and efficiency of N.

Arbuscular mycorrhizal (AM) fungi forms a beneficial symbiosis with roots, there by increasing root surface area which assists roots in exploring larger soil volumes there by bring more ions closer to roots and contributing to higher nutrient inflow (Sanders et al., 1977; Smith et al., 1993). Primary benefits of AM are enhanced acquisition of mineral nutrients, plant tolerance to soil chemical constraints such as acidity, salinity, alkalinity, and increases the ability of the host-plants to withstand or have reduced acquisition of elements toxic to plant growth

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(Marschner and Dell 1994). Other benefits for the host-plants are the improvement of water uptake and the withstanding of drought (Cooper 1984, Nelsen 1987). The AM infection may act as general modifiers of NUE regardless of the extent to which the plant roots are infected and extent of infection appears to be under genetic control and shows considerable variability between crop species/cultivar and AM isolates. (Smith et al., 1993). Such an interaction could be used to select crop cultivars and effective AM isolates to enhance nutrient uptake from nutrient deficit or low input systems. The P uptake in plant is most affected by AM interaction, but AM can also directly increase the uptake of Zn, Cu, N, and the cation/anion ratio. (Abbott and Robson 1984).

Weeds compete with crop plants for water, nutrients, and sunlight, thereby reducing crop yields and consequently NUE. Allelopathic interactions of weed-crop plants are quite common. Appropriate crop rotation is an effective way to alleviate weed and allelopathic problems (Fageria, 1992).

Infections of diseases and insects also reduce crop yields and consequently NUE (Fageria, 1992; Lyda, 1981). Soil borne pathogens such as actinomycetes, bacteria, fungi, nematodes, and viruses present in the soil around roots lead to pathogenic stress and bring profound changes in the morphology and physiology of roots and shoots that reduces plants ability to absorb and use nutrients effectively (Lyda,1981, Fageria et al., 1997a, Fageria, 1992). Proper biological, chemical, physical, and cultural management practices can be used to alleviate the pathogenic stress (Lyda, 1981). Diseases and insects that infect plant leaves, reduce photosynthesis activity resulting in lower utilization of absorbed nutrients (Fageria, 1992). Plant diseases are greatly influenced by environmental factors, including deficiencies and /or toxicities of essential nutrients (Huber, 1980). Balanced nutrition has an important role in determining plant resistance or susceptibility to diseases. The severity of obligate and facultative parasites on plants is influenced by the level of N available to plants and the lack of soil P. These are the main factors in determining the severity of fungal diseases, pythium rot, and viral diseases (Engelhard, 1989; Graham and Webb, 1991; Huber, 1980). Lack of Ca, Mg, Zn, B, Mn, Mo, Ni, Cu, Fe, and Si, are known to induce various diseases in plants (Engelhard, 1989; Fageria et al., 1997a; Graham and Webb, 1991; Huber, 1980).

Climate Factors

Temperature, solar radiation, and precipitation during crop growth influences nutrient availability in soil and the plants ability to take up and utilize the nutrients and subsequent yields (Arkin and Taylor, 1981; Baligar and Fageria, 1997; Barber, 1995; Fageria, 1992 Fageria et al., 1997a; Marschner, 1995). To improve NUE in plants we need to optimize best management practices that con-

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sider climatic variables based on specific needs of a given species/cultivar. Soil temperature influences the rate of nutrient release from organic and inorganic reserves, and the uptake by roots and subsequent translocation and utilization in plants (Arkin and Taylor, 1981; Cooper, 1973). Solar radiation has a direct effect on photosynthesis which in turn influences a plants' demand for nutrients. The quality of radiation and crop shading reduces crop growth, N_2 fixation and ion uptake (Fageria 1992). Total rainfall is not as important for crop production and higher NUE as is the distribution of rainfall during the growing season and how fertilizers interact with the water balance of the root zone. To a larger extent, climatic variables cannot be changed; but cultivar selection and crop management must be tailored to prevailing climatic conditions. In a breeding program it is vital to include physiological traits that improve the plants ability to tolerate multiple climatic stress factors.

CONCLUSIONS

Increased NUE in plants is vital to enhance the yield and quality of crops, reduce nutrient input cost and improve soil, water and air quality. The definition of NUE in plants need to be clearly defined and carefully selected to reflect the end use. Much can be achieved by selecting nutrient efficient genotypes and to incorporate these in breeding programs. However, the poorly developed state of nutritional genetics of plants and its response to environmental variables and management practices and the difficulty of identifying nutrient efficiency traits by rapid and reliable techniques have contributed to a lack of progress and success in breeding plant cultivars with high NUE.

Plant species and cultivars within species differ in absorption and utilization of nutrients and such differences are attributed to morphological, physiological and biochemical processes in plants and their interaction with climatic, soil, fertilizer, biological and management practices. An improved NUE in plants can be achieved by careful manipulation of plant, soil, fertilizer, biological, environmental factors and best management practices. There is great need for a well coordinated, multi-disciplinary, team effort of plant geneticists and breeders, physiologists, biologists, agronomists, soil scientists, and chemists among other disciplines, to formulate an effective system to over come the internal and external constraints that are contributing to lower nutrient use efficiencies and to make increased NUE in plants a reality.

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