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NUTRIENT INTERACTIONS IN CROP PLANTS

V. D. Fageria

Department of Agronomy, Rajasthan Agricultural University, Agricultural Research Station, Durgapura, Jaipur-302018, India
E-mail: root@rauars05.raj.nic.in

ABSTRACT

Balanced supply of of essential nutrients is one of the most important factors in increasing crop yields. The objective of this review is to discuss interactions among major and minor nutrients in crop plants. In crop plants, the nutrient interactions are generaly measured in terms of growth response and change in concentration of nutrients. Upon addition of two nutrients, a increase in crop yield that is more than adding only one, the interaction is positive (synergistic). Similarly, if adding the two nutrients together produced less yield as compared to individual ones, the interactions is negative (antagonistic).When there is no change, there is no interaction. All the three interactions among essential plant nutrients have been reported. However, most interactions are complex. A nutrient interacting simultaneously with more than one nutrients. This may induced deficiencies, toxicities, modified growth responses, and/or modified nutrient composition. Better understanding of nutrient interactions may be useful in understanding importance of balanced supply of nutrients and consequently improvement in plant growth or yields.

INTRODUCTION

Interaction between nutrients in crop plants occurs when the supply of one nutrient affects the absorption and utilization of other nutrients. This type of interaction is most common when one nutrient is in excess concentration in the growth medium (1). Nutrient interactions can occur at the root surface or within the plant and can be classified into two major categories. In the first category are interactions which occur between ions because the ions are able to form a chemical bond. Interactions in this case are due to formation of precipitates or complexes. For example, this type of interaction occurs where the liming of acid soils decrease the concentration of almost all micronutrients except molybdenum. But this decrease varies from nutrient to nutrient. For example, Cu is more strongly complexed by soluble organic matter than zinc (2), and effects of increasing soil pH are more marked on Zn uptake than Cu uptake by plants (3). The second form of interaction is between ions whose chemical properties are sufficiently similar that they compete for site of adsorption, absorption, transport, and function on plant root surfaces or within plant tissues. Such interactions are more common between nutrients of similar size, charge, geometry of coordination, and electronic configuration (3). This type of interaction is common among Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}.

Hiatt and Leggett (4) suggested that cation-cation and anion-anion interactions occur mostly at the membrane level and are primarily of a competitive nature. Cation-anion interactions occur at both the membrane and in cellular processes after absorption. These cellular interactions are less understood. Epstein (5) pointed out that the cation content of plant material is dependent on both the availability of the particular cation and the presence or absence of other cations in the growth medium. Generally an excess of one cation in the nutrient medium reduces the net uptake of other cations, whereas the sum of cations in the plant tissue often remains nearly constant. This phenomenon is called cation antagonism (6).

Nutrient interactions may be positive or negative and also possible to have no interactions. When nutrients in combination results in a growth response that is greater than the sum of their individual effects, the interaction is positive. When the combine effect is less, the interaction is negative. In the former case the nutrients are synergistic, whereas in the latter they are antagonistic. If there is no deviation from two nutrients additive response when applied separately, absence of interaction (7,8). However, in most of the plant nutrition experiments, influence of single nutrient on plant growth is studied. Data related to effects of more than one nutrient on plant growth in the same experiment are limited. Under this situation, nutrient interactions can be identified taking into consideration effects of increasing nutrient concentrations on the uptake of other nutrients and corresponding plant growth. Where, plant uptake of a given nutrient start decreasing and corresponding growth is also decreased, there is negative interaction between the two nutrients. If the plant growth is incraesed with increasing nutrient concentration in the growth medium, and uptake of a given nutrient also increased, the interaction is positive.

Nutrient interaction is influenced by factors such as concentration of nutrient, temperature, light intensity, soil aeration, soil moisture, soil pH, architecture of root, the rate of plant transpiration and respiration, plant age and growth rate, plant species and internal nutrient concentration of plants. As interaction occur, changes are initiated at the subcellur level which may ultimately be manifested through changes in rates of respiration, photosynthesis, cell division and expansion, utilization, and translocation of carbohydrates and organic acids. The net influence of these interactions and processes produces the final yield of a crop. The objective of this review is to emphasises the importance of interactions among macro and micronutrients in the production of annual crops. This information may improve the understanding of nutrient balance for optimum plant growth.

Nitrogen Versus Other Nutrients

Nitrogen (N) plays a pivotal role in the plant metabolism and hence in detremining growth. The inorganic nutrition of plants has, therefore, been dominated by the N, as it improves both quantity and quality of the produce. Under these situations understanding N interactions with other essential plant nutrients is fundamental importance in improving plant growth and development. Increasing N supply enhances growth, and consequently, increases the demand for other nutrients. This demand can translate into plant concentrations less or greater than that needed for sufficiency, depending on the nutrient supply in the root zone (9). Numerous workers have reported positive interaction between N and phosphorus (P) which leads to increase in P absorption and higher yields (10,11). The mechanisms involved are not well understood, but a number of both soil and plant related mechanisms have been proposed (11). Wilkinson et al. (9) reported that N can increase P uptake in plants by increasing root growth, by increasing the ability of roots to absorb and translocate P, and by decreasing soil pH as a result of absorption of NH_4^+ and thus increasing solubility of fertilizer P.

Kawasaki (12) reported that in rice, barley, corn, cucumber and tomato, Ca content was higher when ($NO_3{-}N$) as a nitrogen source in nutrient solution, compared to the supply of NH_4-N. This is due to the inhibiting effect of NH_4-N on the Ca absorption. Botanical cycling between grass and legume components, caused by variations in soil N, constitutes an important interaction in livestock production (13). The ability of grasses with their extensive fibrous root systems to exploit soil supplies of nutrients such as P and potassium (K) can also bring about deficiencies in the associated legume which may reduce its competitiveness in multiple species production situations (9). Kemp (14) reported that increasing N concentration in growth medium can increase or decrease K concentration in the plant tissue depending on K level. Higher K level incraesed K uptake and lower K level decreased uptake of this nutrient. Nitrogen interactions with micronutrients occur due to change in pH in the rhizosphere, with the forms of N used. If N form is NH_4^+, du to cationic absorption, soil pH may decrease and uptake of some micronutrients increases. If the N form is NO_3^-, due to higher uptake of anion, soil pH may incrase and uptake of most micronutrients decreases.

Assimilation of N and sulfur (S) in plants is closely associated (15). Nitrogen nutritin has a strong regulatory influence on S asimilation and vice versa (16,17). The majority of S in plant tissue is present, mainly as protein-S, in the organic pool. A review by Dijkshooron and van Wijk (18) revealed that, although the ratio of total N to total S $(N/S)_t$ varied widely, under adequate nutritional conditions the ratio of organic N to organic S remained rather constant at about 17.5 in legumes and 13.8 in graminaceous plants. The N to S ratio have since been widely used to diagnose S status of crops. When the S supply is adequate, sulphate and other non-protein S compounds accumulate in vegetative tissues, resulting in $(N/S)_t$ ratios smaller than the protein N/S ratio $[(N/S)_p]$. When S is deficient, non-protein N compounds accumulate, causing $(N/S)_t$ ratios to become greater than $(N/S)_p$. Evidence is present that $(N/S)_p$ ratios are relatively constant in the vegetative tissues of the crops with a low S requirement (19). Randall et al. (20) showed that $(N/S)_p$ of wheat grain varied from 12 to 25 as a result of varying N and S supply.

Micronutrient interactions with N occur frequently due to change in soil pH with the addition and uptake of NH_4^+ and NO_3-N. When more NO_3- is applied or present in the soil, its uptake increased as compared to NH_4^+-N, and rhizosphere pH increases. When more NH_4^+ is absorbed, soil pH decreases. Differences in Fe uptake in rice grains at various N levels were highly significant and indicated that Fe increased with the addition of N as NH_4^+. However, Zn concentration did not increase with the addition of N (21). Other interactions of N with micronutrients occur when N stimulated growth causes increased demand for a nutrient and possible deficiency. Such effects may occu with boron (B), copper (Cu), manganese (Mn), and molybdenum (Mo) where cation competition between NH_4^+ and Cu^{2+}, Mn^{2+}, and Zn^{2+} for absorption can occur (9). Nitrogen fertilization particularly as NH_4^+ has been found to help overcome yield reducing effects of salinity (22).

Phosphorus Versus Other Nutrients

Phosphorus deficiency is a principal yield limiting factor for annual crop production in acid and alkaline soils of temperate as well as tropical regions (1,23). This means, evaluating interaction of phosphorus with other nutrients is very important to maintain a balanced nutrient supply for improving crop yields. Generally, phosphorus has positive significant interaction with N absorption and plant growth (7,10). It is commonly held view that increased growth requires more of both N and P, the inference being that mutually synergistic effects result in growth stimulation and enhanced uptake of both elements (7).The mechanisms involved are not well understood, but a number of both soil and plant related mechanisms have been proposed (11).

Positive interactions between P and Mg are expected since Mg is a activator of kinase enzymes and activates most reactions involving phosphate transfer.

If large amounts of P are supplied, however, luxury uptake of P may occur (24), an effect that raises the ratios of P to iron (Fe) (25) and zinc (Zn) in plant tissues (26,27) and has often been associated with deficiency symptoms of the two micronutrients (28). Yet it is not clear whether the major interaction take place in the plant or in the soil. Indeed, large P-inputs decrease soil Zn diffusion rates and enhance Fe immobilization. Positive interaction between P and Mn has been reported in the literatuer (29) and is assumed to be attributed to the soil-acidifying effect of P, which increases the Mn uptake (30).

Application of phosphatic fertilizers at a high dose increases the severity of such deficiency in soils that are low or marginal in available Zn. Various hypotheses have been suggested to explain this phenomenon, which include (i) interaction of P with Zn in soil (31), (ii) interference of P at the level of plant metabolism involving uptake, translocation, and utilization of Zn (32), and (iii) imbalance of P:Zn ratio due to increased dry matter production with P application. Although it is recognized that major interactions between P and Zn occur at the plant metabolic level, the importance of this interaction in the soil has also been reported (33). Saeed and Fox (34) observed an increase in Zn sorption in Hawaiian soil due to P fertilization. They suggested that sorption of P on the surfaces of Fe and Al oxides increased negative charges on them resulting in a increased sorption of Zn.

Iron deficiency induced by heavy applications of P has been reported (7,35). Interaction of P and Fe leading to Fe chlorosis appears to be caused by an internal immobilization of Fe probably due to formation of Fe phosphate (36). Other mechanisms of Fe reduction by P application may be inhibition of Fe absorption by roots and of Fe transport from roots to shoots, and inactivation of plant Fe (37,38).

Potassium Versus Other Nutrients

Potassium is unique the essential nutrients in the diversity of roles it plays in plant metabolism processes (6). Activation of enzymes, acting as an osmoticum to maintain tissue turgor pressure, regulating the opening and closing of stomates, and balancing the charge of anions (particularly organic acids synthesized during carbohydrate metabolism) are physiological functions of K in plant cells (39,40,41). Adequate K level is essential for the efficient use of N in crop plants. Potassium could be involved with NO_3^- uptake, the predominant form of soil N, through two processes. First, K has been found to co-transport in the xylem with NO_3^- as an accompanying cation from the roots to aerial plant parts and then recycle down the phloem with malate (42). Secondly, because NO_3^- is taken up by plant roots via an active process (41), NO_3 uptake may be affected through the influence of K on the translocation of photosynthetic assimilates, needed to support this active uptake process (43).

Potassium has antagonistic effects on the absorption of Ca^{2+} and Mg^{2+} at higher concentration wich depends on plant species and environmental conditions. Fageria (44) studied potassium interaction with P, calcium (Ca), and magnesium (Mg) in rice plants grown in nutrient solution (Table 1). There was a significant quadratic decrease in the uptake of P and Ca with increasing K concentration in the solution culture. However, Mg uptake was increased at the

Table 1. Phosphorus, Calcium, and Magnesium Content in the Shoots of Rice Plants Under Different Potassium Concentrations in Nutrient Solution

K Conc. (μM)	P (mg kg^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})
51.14	4.86	7.77	3.42
102.29	4.40	6.62	4.12
128.87	4.10	6.29	4.65
179.01	3.66	5.35	5.27
255.74	3.10	4.54	4.85
511.48	3.10	3.75	2.85
767.22	2.50	3.68	2.77
1534.44	2.40	3.32	2.60
Regression			
β_0	4.7020	7.3576	4.7186
β_1	−0.00463	−0.00883	0.00301
β_2	−0.00463	−0.00883	0.00301
R^2	0.8866**	0.8762**	0.5106^{NS}

^{*,**,NS}Significant at the 5 and 1% probability levels and nonsignificant, respectively.
Source: Fageria (44).

lower K concentration and only decreased at the higher concentration. But the effect was statistically nonsignificant. Higher absorption of P and Ca in the lower concentrations of K is believed to be due to high mobility of K, which when present in the higher concentrations will tend to depress the absorption of other ions (45,46). The decrease in Ca uptake with increasing K concentrations may be related to competition between K and Ca due to physiological properties of these ions (47,48). The depressing effect of K on uptake of Mg at higher concentrations may be interpreted as a result of competition for metabolically produced binding compounds (49). Hannaway et al. (50) reported that increasing the level of K decreased the Mg concentration and accumulation in tall fescue shoots, but did not affect its influx into the roots. Reduced translocation from the roots to the shoots appeared to be the source of the K/Mg antagonism.Grunes et al. (51) found that K fertilization significantly increased K tissue concentrations at the expense of Mg and Ca concentrations in three cool season grasses accompained by increased concentrations of organic acids which may impact the bioavailability of Mg to livestock.

Gupta (52) reported decreased B levels in plants with added K or when grown on soils with high K levels. Smith (53) working with alfalfa adequately fertilized with P, reported that K topdressing reduced Cu^{2+} levels in the forage. Bolle-Jones (54) studied potato fertilization in pot sand culture and found that added K^{+} reduced mild Fe^{2+} deficiency synptoms. Ramani and Kannan (55) noted that K^{+}, Ca^{2+}, and Mg^{2+} play a significant role in regulation of Mn^{2+} absorption by plants. The cations either promote the absorption when Mn^{2+} is present in low amounts or effectively decrease Mn^{2+} uptake when it is present in high amounts that might be toxic. Shukla and Mukhi (56) reported that Zn^{2+} utilization by corn increased with increasing rates of K^{+}.

Calcium, Magnesium, and Sulfur Versus Other Nutrients

Iron-chlorosis is a world-wide problem, particularly in arid and semi-arid regions. The soils of these naturally dry ares are of lime-induced chlorosis and frequently contain high concentration (more than 20%) of calcium carbonate. Although, iron is abundant in these soils, it is not readily available for uptake to crop plants. Calcium content of gramineous plants is generally lower than dicotyledonous plants (12). Ishizuka and Tanaka (57), studied interactions of Ca with other nutrients and reported that Ca stimulated the absorption of P and K under certain concentration ranges of ions in nutrient solution. Phosphorus uptake by rice plants in nutrient solution was significantly decreased with incresing Ca concentration (Table 2). Similarly, uptake of K and Mg were also decreased at higher ca concentration, however, effects were statistically nonsignificant. The inhibiting effect of higher Ca concentration on the uptake

Table 2. Phosphorus, Potassium, and Magnesium Content in Shoots of Rice Plants Under Different Calcium Concentrations in Nutrient Solution

Ca Conc. (μM)	P (mg kg^{-1})	K (mg kg^{-1})	Mg (mg kg^{-1})
6.23	5.04	26.40	3.87
12.47	4.95	27.20	4.62
49.90	5.05	27.40	5.34
74.79	4.69	31.20	5.40
124.75	4.49	31.50	5.46
249.50	3.75	29.20	4.74
499.00	3.50	25.00	3.99
748.00	3.37	23.90	3.98
Regression			
β_0	5.1166	28.0947	4.8111
β_1	−0.00591	0.00923	0.00105
β_2	0.0000048	−0.000021	−0.0000032
R^2	0.9676**	0.5220^{NS}	−0.0000032^{NS}

^{**,NS}Significant at the 1% probability level and nonsignificant, respectively.
Source: Fageria (44).

Table 3. Uptake of P, K, and Mg by Dry Bean Plants Under Different Ca Concentrations

Ca Conc. (cmol$_c$ kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Mg (g kg^{-1})
4.9	2.1	32	8.3
10.0	1.8	34	4.6
11.4	1.4	28	3.4
12.3	1.4	25	3.3
12.5	1.1	29	2.6
Regression			
β_0	1.3482	13.9272	11.8220
β_1	0.2607	5.4567	−0.7223
β_2	−0.0218	−0.3570	
R^2	0.9366**	0.6826^{NS}	0.9900**

^{**,NS}Significant at the 1% probability level and nonsignificant, respectively.
Source: Fageria and Baligar (58).

of K and Mg may be related to decrease in the permeability of cells (44). Fageria and Baligar (58) studied the interactions between calcium and other nutrients P, K, Mg, Zn, Cu, Mn, Fe, and B in dry bean grown on an Inceptisol (Tables 3 and 4). The uptake of all these nutrients was significantly affected by increasing Ca

Table 4. Uptake of Zn, Cu, Mn, Fe, and B by Dry Bean Plants Under Different Ca Concentrations

Ca Conc. ($cmol_c\,kg^{-1}$)	Zn ($mg\,kg^{-1}$)	Cu ($mg\,kg^{-1}$)	Mn ($mg\,kg^{-1}$)	Fe ($mg\,kg^{-1}$)	B ($mg\,kg^{-1}$)
4.9	70	9	4333	327	33
10.0	26	5	107	107	19
11.4	15	5	40	93	20
12.3	14	4	40	107	17
12.5	13	4	30	83	14
Regression					
β_0	106.1109	12.0731	6863.8470	466.5526	43.7269
β_1	−7.6820	−0.6529	−582.5682	−31.6196	−2.2629
R^2	0.9840^{**}	0.9741^{**}	0.9101^{**}	0.9235^{**}	0.9428^{**}

**Significant at the 1% probability level.
Source: Fageria and Baligar (58).

concentration in the growth medium. The concentrations of P and K were quadratically increased, whereas, concentrations of Mg, Zn, Cu, Mn, Fe, and B significantly decreased as soil Ca content increased from 4.9 to 12.5 $cmol_c\,kg^{-1}$ of soil. Similarly, Fageria and Baligar (58) also reported decrease in concentrations of Mg, Zn, Mn, and Fe in wheat and soybean plants with increasing Ca content in the soil. Calcium silicate is known to reduce Fe and Mn toxicity in lowland rice. Silicon increases the oxiding power of the roots making Fe and Mn less soluble. Addition of Ca to saline irrigation water affects nutrient uptake, at least partly by modifying root function resulting in reduced uptake of heavy metals even though their solubility may not be appreciable in Saline water (59).

Magnesium significantly decreased the uptake of K and Ca in the rice plants grown in nutrient solution. However, uptake of P was not influenced by increasing Mg conentration in the culture solution (Table 5).The depressive effect of Mg on uptake of K and Ca may be interpreted as a result of competition for metabolically produced binding compounds (44). Soliman et al. (60) reported that the acidifying effect of S applications to a highly calcareous soil was important in the mobilization of Fe, Mn, Zn, and P and availability of these nutrients to crops.

Micronutrients Versus Other Nutrients

Role of micronutrients in crop production has significantly increased in the recent years due to availability of better analysis techniques and better understanding of their functions in crop plants. However, still lack of sufficient

Table 5. Phosphorus, Potassium, and Calcium Content in Rice Shoots of Rice Plants Under Different Magnesium Concentrations in Nutrient Solution

Mg Conc. (μM)	P ($mg\,kg^{-1}$)	K ($mg\,kg^{-1}$)	Ca ($mg\,kg^{-1}$)
8.33	2.58	35.50	5.86
16.45	3.01	34.00	5.66
24.27	3.29	33.50	5.26
32.90	3.32	32.66	5.13
41.11	4.16	31.20	4.86
82.26	3.20	27.76	4.86
123.39	3.25	22.00	4.53
205.65	3.19	11.70	4.00
Regression			
β_0	2.9724	36.4438	5.7454
β_1	0.00998	−0.11833	−0.01514
β_2	−0.000045		0.000033
R^2	0.1549^{NS}	0.9960^{**}	0.8943^{**}

^{**,NS}Significant at the 1% probability level and nonsignificant, respectively.

experimental data to conclude micronutrients effcets on uptake and utilization of other essential plant nutrients. Deficiency or toxicity of micronutrients in crop plants are more often caused by their form of existence or interactions with other soil properties in the soil, rather than merely by their individual concentration in a greater or lesser amount. This means, whether micronutrients are in deficiency or in excess for plants, it is necessary to examine not only the critical levels of the absolute concentration of the elements contained in the soil, but also the soil physical, chemical and biological properties.

Iron Versus Other Nutrients

In field conditions, an interaction among iron and other elements absorption has been reported (61). High levels of several minerals (Ca, P, N, Mn, and Cu) in soil contributing to iron chlorosis presumably because they are involved in interaction with iron nutrition, although iron deficiency per se may inhibit absorption of some elements (62). In flooded rice, iron toxicity is a common phenomenon due to reduced soil conditions, where, Fe^{3+} reduced to Fe^{2+} and iron concentration in the soil solution and plant increased (35). When Fe toxicity occurs in rice plant, the Fe concentration in leaf blades is reported to be more than 300 $mg\,kg^{-1}$ (35,63). The nutritional status of the rice plant is related to iron toxicity. Phosphorus, K, Ca, Mg, and Mn deficiencies decrease the Fe excluding power of rice roots and thereby the Fe toxicity is caused through an excessive Fe uptake. Adequate concentration of K in the soil solution significantly decreased Fe toxicity due to improving respiration capacity of rice roots (35). Luo et al. (64) reported that excessive Fe^{2+} reduces N, P, K, and Mg uptake in rice genotypes. The nutrient element concentrations, however, were still higher above deficient criteria even in severely affected plants, suggesting that the retardation of growth may not be intirely due to the deficiency of these elements in plants at the seedling stage. These authors also reported a significant correlations between the genotypic variation and the decrease in N, P, K, and Mg uptake and their tolerance to Fe^{2+} toxicity, which suggests that the ability to maintain higher nutrient element under a Fe^{2+} toxic condition contributes the tolerance to Fe^{2+} toxicity condition. Iron toxicity is more severe on heavy textures soils as compared to light textured soils. However, there exist a varietal difference in the tolerance to fe excess as well as in the Fe-uptake ability of rice (65). Fageria et al. (35) reported that the addition of MnO_2 were attributed to an increase in the redox potential and reduced concentration of Fe^{2+} and organic reduction products.

Nutrient uptake inhibition under different concentrations of iron was reported by Fageria and Rabelo (65) for rice plants grown in nutrient solution. Among macronutrients, P uptake was most affected, followed by K, Mg, N, and Ca . Thus, in soils where problems of Fe toxicity exists, P and K deficiency will occur first, uptake of Mn was highly reduced, followed by Zn and Cu. Fageria (66) also reported that the uptake of P, K, Ca, Mg, and S by alfalfa, wheat, rice and red clover was decreased by increasing Fe levels in the growth medium. Similarly, in alfalaf, red clover, and wheat uptake of Mn, Zn, and Cu were decreased when Fe concentration in the nutrient solution was higher than 320 μM.

Ali et al. (67) reported that application of $25\,mg\,Fe\,kg^{-1}$ resulted in significant increase of N, P, K, Zn, Cu and Mg concentration with or without N fertilization, however, it significantly depressed the concentration of Ca and Mn in the leaf blades of groundnut. Negative interactions between Fe and Mn have been widely reported in crop plants (68,69). Among other nutrients which interfere with Fe nutrition, N, especially nitrate uptake is known to aggravate chlorosis by raising soil pH (70,71). Olsen and Watanabe (72) reported that an increase in Mo decreased Fe uptake. This interaction may be important in alkaline soils in which Fe availability may be low and soluble $MoO_4{}^{2-}$ concentration high.

Manganese Versus Other Nutrients

Manganese concentration in the plant tissue for normal growth is the range of 50 to $100\,mg\,kg^{-1}$ dry weight (73). Manganese plays an important role in the metabolism of plants, particularly in processes of activation of different enzymes, chlorophyll synthesis and photosynthesis (74). In leaf tissues, manganese is associated with proteins of the oxygen evolving system and is indispensable for the generation of the photosynthetic energy flow (75). The photosynthetic electron transport is affected when Mn deficiency occurs, since the first step of the electron transport chain is impaired (76). Under field conditions manganese deficiency is usually confined to plants growing in highly leached tropical soils or high-pH soils with a large organic matter content (1). Studies on the interaction between Mn uptake and other divalent cations have been reported (77,78,79). Chinnery and Harding (78) reported that higher concentration of iron in soybean leaves at lower Mn concentration. They found that the concentration and amount of manganese in the soybean shoots decreased with increased iron concentration in the solution, probably an oxidation of iron by manganese.

Excess Mn has induced Fe deficiency in potatoes grown in nutrient culture and produced Mn/Fe ratios of 18 or more in plant tops (80). Aluminum counteracted these effects by increasing Fe content of plants and decreasing Mn/Fe ratios. Leach and Taper (81) concluded that the optimum Fe/Mn ratios in plants ranged from 1.5 to 3.0 for kidney beans and from 0.5 to 5.0 for tomato. Iron deficiency developed at lower ratios and Mn toxicity at higher ratios. Tanaka and Navasero (82) concluded that Mn toxicity symptoms and Fe deficiency symptoms are different in rice and that the range within which Fe toxicity can b remedied by Mn applications is narrow. Manganese absorption in tomato is influenced by interactions between Fe, Mn, and Mo (83). Added Fe counteracted the yield depressive effects of added Mn, but the amount of Fe needed for maximum yield was increased as the Mo supply increased. At low Fe levels Mo decreased yields. At higher Fe levels Mo increased yields. Brown and Jones (84) suggested that high Fe levels in the tops of Fe-inefficient, Mn sensitive, soybean may accentuate Mn toxicity or create Fe toxicity per se. They also speculated that high K levels in the tops of Mn-tolerant soybean alleviate the harmful effects of high internal Mn concentrations.

Increased Ca levels in the growth medium often decrease Mn uptake and toxicity (85). Heintze (86) concluded that P detoxifies Mn by precipitation within plant roots. There is abundant evidence that a soluble source of silicon (Si) in the growth medium can protect plant against Mn toxicity (87). Lewin and Reimann (88) reported that Si-deficient plants accumulated higher Mn concentrations than Si-sufficient plants. Silicon decreased excessive uptake of both Mn and Fe (87).This means that toxicity of Mn in the growth medium or even within the plant depends upon interactions between Mn and several other elements, particularly Fe and Si.

Increasing Mn concentrations in nutrient solution triggered a general synergistic effect on Ca, Mg, sodium (Na), P, and Cu net uptake, but displayed an antagonistic action on K and Zn in rice plants. The net translocation rate of Fe was also inhibited (89). Concerning to the crop, increasing Mn concentrations delayed its maturation, being the levels of nutrients accumulation also changed. However, the concentration of potentially toxic metals inthe grain was much lower that in vegetative plant tissues. The concentrations of Ca, K, Na, P and Zn interacted with increasing Mn concentrations mostly in a manner to that of the shoot, but a different pattern was found for mg, Cu, and Fe. Manganese uptake was reduced with application of Zn fertilizers (32). Sims et al. (90) observed that Mn concentrations were reduced in half by Mo fertilization.

Copper Versus Other Nutrients

The use of fungicides containing Cu began in the 19th centuary and its importance has increased in recent years, specially in cereal crops. Copper content in the plant tissue is in the range of 5 to 20 $mg\,kg^{-1}$ dry weight, which is the second lowest next to Mo among the micronutrients (73). Several factors influence the level of available copper in soil. Such factors may be enumerated as total Cu content, soil organic matter level (91); clay type and content (92,93); oxide type and content (94); redox potential (95); microorganisms and nature of other elements associated with copper (94,96). Copper in excess interfers with plant's capacity to absorb and/or translocate other nutrients (97) inhibiting root elongation and adversely affecting the permeability of the root cell membrane (98). Copper in excess also has a destructive effect on the integrity of the chloroplast membrane, leading to a decrease in photosynthetic activity (99).

Zinc Versus Other Nutrients

Zinc content in the plant tissue is in the range of 30 to 100 $mg\,kg^{-1}$ dry weight under normal plant growth (73). Foy et al. (87) reported that increased soil Zn greatly increased translocation of Mn to soybean tops. They hypothesized that Zn and Mn interfere with Fe utilization in the leaves for chlorophyll synthesis. Further, a Zn-induced Mn toxicity symptoms (crinkle leaf) was seen in soybean (87). Zinc interaction with B has been reported and it reduces the toxic effetcs of excessive boron in crop plants (100,101).

Boron Versus Other Nutrients

Singaram and Prabha (102) studied boron and calcium interaction in tomato plants and reported that the translocation of absorbed Ca to the aerial parts of the plant was a problem due to the relatively high pH of the translocating plant sap. But this was obviated by applied B which helped translocation of absorbed Ca. As the Ca concentration decreased the B concentration increased in the root and this was not found in shoot and fruit indicating that B translocation was not hindered by Ca in calcareous soil. On the basis of equivalent Ca/b ratio, application of B both foliar (0.3%) and soil (10 kg ha^{-1}) could ensure adequate B in shoot alleviating excess Ca in soil.

Molybdenum Versus Other Nutrients

Molybdenum is an essentail micronutrient of higher plants. Although Mo requirement of higher plants is very small, it has crucial roles in higher plants, mainly via molybdoenzymes. Nitrate reductase, an important molybdoenzyme, catalyzes the rate-limiting step of nitrate assimilation (103,104). Molybdenum deficiency occurs in highly acidic soils that are strongly weathered and leached and in soils in which the element is in an unusable form. Sulfur application may decrease Mo concentrtion in plants (105). Concentrations of tissue Mo resulting from application of 0.5 and 1.0 mg Mo kg^{-1}, which were reportedly toxic to

Table 6. Balanced Uptake Requirements of N, P, and K for Irrigated Lowland Rice

	Required Nutrient Uptake (kg ha^{-1})		
Grain Yield (t ha^{-1})	N	P	K
1	15	2.6	15
2	29	5.2	29
3	44	7.8	43
4	59	10.4	58
5	73	13.0	72
6	88	15.6	87
7	104	18.4	103
7.5	115	20.4	114
8	127	22.6	126
8.5	142	25.1	140
9.0	159	28.2	157
9.5	182	32.2	180
9.8	205	36.3	203
9.9	217	38.6	215
10.0	243	43.1	240

Source: IRRI (21).

animals, were corrected by soil application of 50 to 200 mg S kg^{-1}. Phosphorus generally increases the availability of Mo. This increase in Mo availability may be in part to the reduced adsorption of Mo by soil when P is applied (106).

Chlorine Versus Other Nutrients

Limited data are available on interaction of chlorine with other nutrients. Chlorine is highly mobile in the soil, and excessive concentrations can be leached from the soil by overhead irrigation or in humid and sub-humid climate by rainfall. High concentration of Cl^- in the soil solution may depress nutrient-ion activities and produce extreme ratios of Na^+/Ca^{2+}, Na^+/K^+, $Ca^{2+}Mg^+$, and Cl^-/NO_3^-. As a result, the plant becomes susceptible to osmotic and specific-ion injury as well as to nutritional disorders that may result in reduced yield or quality (107).There is evidence that when Cl^- rather than SO_4^{2-} is the anion in saline soils, Ca deficiency could be alleviated (108).

CONCLUSIONS

The recognition of the importance of nutrient balance in crop production is an indirect refelection of the contribution of interactions to yield. Table 6 shows the balanced N, P, and K uptake requirements for irrigated lowland rice. The highest yields are obtained where nutrient and other growth factors are in a favourable state of balance. As one moves away from this state of balance, nutrient antagonisms are refelected in reduced yields. Antagonistic as well as synergistic interactions are determined by level of each nutrient in the soil and plant species and sometimes even among cultivars of the same specie. In addition, soil physical, chemical and biological properties also change the patterns of nutrient interactions in crop plants. Better understanding of these soil properties can lead to reduce negative interactions and more efficient crop production. Although many studies have been reported, the interactions are not fully characterized. The interactions between macro and micronutrients need more study and characterization, especally under field conditions.

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