2. Micronutrient needs of tropical food crops

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The essential micronutrients are copper, zinc, manganese, iron, boron, and molybdenum; chlorine is also essential but will not be discussed here since it is rarely lacking in agricultural systems. These micronutrients are essential for plant survival but are only needed in small quantities. In this chapter we will examine the micronutrient needs of tropical food crops. We will review the factors that control micronutrient uptake, the crop's response to this uptake, and the way in which the tropical climate and crop varieties might affect the amounts of micronutrients needed. We will also discuss trends in crop management and yield levels and how these factors affect micronutrient needs.

The tropics are very diverse in both climate and soil resources. The tropics are most commonly defined as the geographic region that extends from 23.5° north to 23.5° south of the equator. This area covers 38% of the land mass area of the world, and it is spread over Africa (43%), South America (28%), Asia (20%), Australia (5%), and Central and North America (4%). Nearly 45% of the world's population lives in this region. The mean monthly temperature of the tropics are 18 °C [27], and generally the temperature is favorable for cropping all the year around. However, moisture often limits the number of crops that can be grown per year, particularly in the dry semiarid tropics and wet-dry semiarid tropics with 2.0–4.5 and 4.5–7.0 wet months, respectively.

Many crops are grown in the tropics, but 12 crops are the most important in food production. These twelve and their production statistics are listed in Table 1. Of these, sorghum, millet, wheat, pulses (cowpeas, pigeon peas, chick-peas, beans), and groundnuts are more abundant in dry semiarid tropics and others in wet-dry to humid tropics. In the economy of the tropics, in addition to these food crops there are a number of important commercial crops such as sugarcane, cotton, coffee, tea, cocoa, coconut, oil palm, and bananas. Although we are not discussing the micronutrient needs of these crops, it needs to be recognized that they all show micronutrient deficiencies and claim higher use of fertilizers, including micronutrients, because of their commercial importance. It may be observed that the average yields of all these 12 food crops are very low, but the potential for increasing production from them in tropical areas is very high. The introduction of high-yielding varieties, particularly of cereals (rice, wheat, sorghum, maize, millets), is opening up new vistas in agriculture in the tropics and providing new opportunities and potential for production.

Tropical crops are not different from temperate crops in their need for micronutrients. However, the tropical climate, soils, cropping systems, and yield levels are usually quite different from those in temperate regions. Although many crop species are common to both regions, including maize, wheat, soybean, potato, and others, the varieties or cultivars are usually different. As we will see there are significant differences between crop cultivars in the efficiency with which they absorb and utilize micronutrients, and these differences may be one valuable tool for increasing food production on some tropical soils.

Role of micronutrients in crops

The role of micronutrients in the plant has been reviewed by several authors in the last 10 years [36, 38, 62]. Since in this respect tropical crops are probably not much different from temperate crops, only a brief overview follows.

Copper

Copper like most cations, is primarily involved with enzyme activity. Several enzymes that are affected directly by copper deficiency have been identified. The physiological result of copper deficiency is an apparent wilting of leaves. Graham [34] suggests that this wilted appearance is the result of structural weakness of the cell walls in copper-deficient plants and is not related to water stress. However, copper deficiency also reduces root growth more than shoot growth, creating an unfavorable shoot:root ratio [16, 49, 66]. This increased shoot:root ratio could lead to plant/water stress. The two phenomena may work together to create the wilted appearance.

Copper deficiency usually delays maturity and reduces yield by reducing grain size [32, 61]. This reduced grain size is attributed to a lower photosynthetic efficiency caused by increased closure of stomata in copper-deficient plants [34]. When stomata are closed, the diffusion of carbon dioxide into the leaves is slowed or stopped. Also, studies with carbon-14 labeled carbon dioxide show that less carbon is fixed in C_6 sugars, the types that are translocated to other parts of the plant in the phloem [12].

Molybdenum

Molybdenum is needed in the least amount of all the essential micronutrients. It is involved in several enzyme systems including nitrogeneous nitrate

Table 1. Production, area, and yield of the major food crops in the tropics in 1981 [30]

Food crop	Area	Production	Yield	World production
	(millions of ha)	(millions of mt)	(mt/ha)	(%)
Rice (*Oryza sativa*)	100	222	2.2	54
Cassava (*Manihot esculenta*)	14	123	9.0	97
Maize (*Zea mays*)	54	79	1.5	18
Wheat (*Triticum aestivum*)	37	61	1.6	13
Sorghum (*Sorghum spp.*)	35	31	0.9	43
Potato (*Solanum tuberosum*)	2	24	10.6	9
Pulses (various species)	48	23	0.5	55
Millet (*Pennisetum* and others)	36	21	0.6	71
Soybean (*Glycine max*)	11	18	1.6	21
Sweet potato (*Ipomoea batatas*)	2	16	6.6	11
Groundnuts (*Arachis hypogeae*)	16	13	0.8	68
Bean (*Phaseolus vulgaris*)	20	9	0.5	65

reductase, xanthine oxidase, aldehyde oxidase, and sulfate oxidase [62]. The result of Mo deficiency is a disrupted nitrogen metabolism. Nitrate reductase activity is reduced by Mo deficiency. Nitrate reductase is involved in the first step of incorporating inorganic NO_3^- into organic N compounds. Das Gupta and Basuchaudhuri [26] demonstrated that Mo applications to rice increased the amount of reduced nitrogen in the plant tissue.

Mo deficiency results in reduced chlorophyll concentration in the leaves [1, 26] which leads to decreased photosynthetic efficiency. The lack of chlorophyll production is most likely a secondary effect of the disrupted N metabolism since Mo has not been shown to play a direct role in chlorophyll synthesis.

Another role of Mo in N metabolism is in N_2 fixation by legume-*Rhizobium* symbioses. Nitrogenase is a Mo-containing enzyme [13, 87]. It catalyzes the fixation of dinitrogen gas to ammonia, which can be utilized by the host plant. However, examples of Mo deficiencies on legumes in the tropics are rare.

Increased use of N fertilizer increases the need for Mo. The production of nitrate reductase by plant is induced by the nitrate availability. Evans [28] showed that NO_3^--grown plants required more Mo and that all the additional uptake was accounted for by the nitrate reductase enzyme.

Iron

Iron is readily oxidized and reduced between its two oxidation states Fe^{3+} and Fe^{2+}. Its role in plant metabolism is closely linked to this reversible Fe^{2+}/Fe^{3+} oxidation. Many of the reactions associated with Fe are the redox reaction of chloroplasts, mitochondria, and peroxisomes [70, 71]. These reactions include coupled electron-transfer reactions (cytochromes a and b), oxidases (cytochrome oxidase), and peroxidases (catalase and peroxidase) [22]. Also, Fe plays a role in the formation of amino levulinic acid, which is a precursor of chlorophyll synthesis [58]. In addition, a strong correlation exists between the leaf chlorophyll and Fe content as shown in Figure 1 [84]. When Fe becomes limiting, thylakoid development (part of the chloroplast) slows or stops. Then, as the leaf continues to expand, the thylakoid constituents such as Fe and several types of chlorophyll are diluted, resulting in the pale yellow color typical of Fe deficiency.

Zinc

Zinc serves both some structural and some regulatory roles in enzyme activity in plant tissue. Only a few enzymes have clearly been identified as requiring Zn; however, for several others there is considerable indirect evidence of Zn involvement [22, 86]. Zn deficiency is characterized by a reduction in the number of ribosomes and RNA in the plant cells. Plant growth is stunted by zinc deficiency. Like most micronutrient deficiencies, Zn deficiency results in an overall reduction in photosynthetic efficiency and disrupted metabolism.

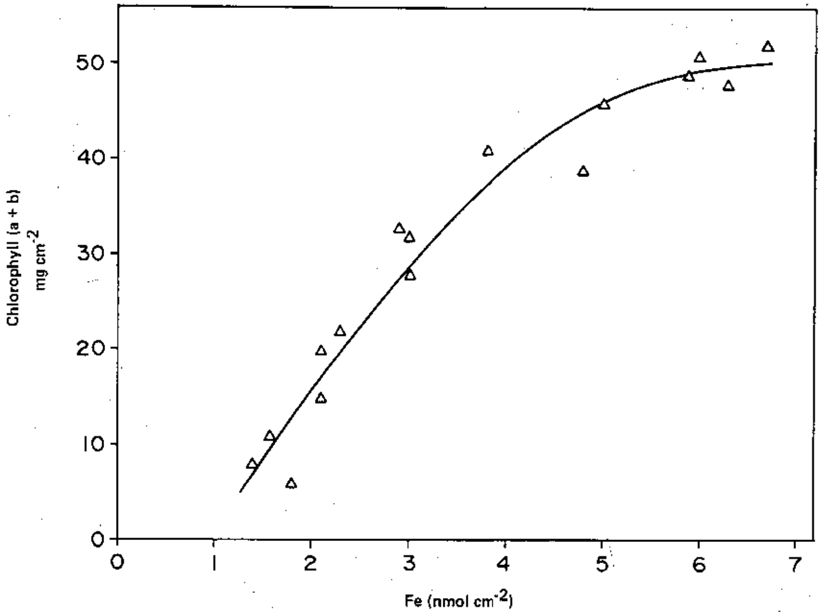

Figure 1. Relationship between leaf iron and chlorophyll contents

Manganese

The role of Mn in plant matabolism is very unclear. Manganese has properties similar to Mg and can substitute for Mg in some enzyme systems. This is probably not a common occurrence in nature since Mg is taken up by crops in much greater quantities than is Mn. Only one system, albeit a very important one, has been shown to require Mn. This is the splitting of water by photolysis in photosystem II [17]. This reaction probably involves a change in the oxidation state of Mn, but the exact structure or functional role of Mn in photosynthesis has not yet been defined.

Boron

The role of B in plant metabolism is not well understood. In fact, no specific function of B has been identified. Only information on the physiological consequence of B deficiency is available to us, and this has been reviewed by Jackson and Chapman [43]. The most pronounced effect of B deficiency on metabolism is a disrupted RNA synthesis. The disruption of RNA metabolism has been studied largely using isotopically labelled RNA precursors in normal and B-deficient plants. An interesting observation is that the results of B deficiency are very similar to those from the application of some plant hormones. This suggests a link between B metabolism and plant hormones. However, our theories of how B functions in plants still have little supporting evidence, and B remains the least understood of the micronutrients.

Species differences

Crop species have shown varying responses to micronutrient availability. A crop such as cassava, which is native to infertile soils, can grow on soil surprisingly low in available micronutrients, whereas crops such as field beans and sorghum seem to require much higher amounts of available micronutrients. Differences between crop species have been recognized for a long time. In 1954, 26 crop species were tested and showed a wide range of sensitivity to Zn deficiency [89]. A more recent complete summary of the likelihood of various crops to respond to micronutrient fertilizer application under conditions conducive to deficiency is shown in Table 2 [54].

Genetic differences between cultivars in their susceptibility to micronutrient deficiencies could be due to several possible mechanisms. Differences occur in (1) the ability to absorb nutrients at low concentration; (2) the excretion of substances by the root to enhance the availability of a micronutrient; (3) the ability to retranslocate ions within the plant; (4) the efficiency of utilization of absorbed nutrients, i.e., the plant's ability to grow well with low tissue concentrations. It is probable that more than one of these mechanisms are responsible for the observed variability.

Table 2. Responses of different food crops to micronutrients under soil or environments favorable to a deficiency [54]

Crop	Zn	Fe	Mn	Mo	Cu	B
Beans	H	H	H	L	L	L
Corn (maize)	H	M	L	L	M	L
Potatos	M	–	M	L	L	L
Sorghum	H	H	H	L	M	L
Rice	M	H	M	L	L	L
Wheat	L	L	H	L	H	L

H = high, M = medium, L = low.

Brown and Jones [8] concluded from their studies that the plant response to micronutrient stress is a genetically controlled adaptive mechanism. The efficient species and varieties exude more H^+ ions and reductants from their roots and thus make some nutrients more available. Christ [19] reported that monocots require higher soil concentrations of iron and are less efficient in iron uptake than are dicots. Much of the difference seems to lie in their abilities to absorb iron in the Fe^{3+} state. In many cultivars severe micronutrient deficiency, such as zinc or iron deficiency, appears in the early stages of growth but disappears or is reduced in intensity with the growth of the root system or rise in temperature. In other cultivars, grown in the same environment, no deficiency symptoms develop. Such cases are common in *rice, sorghum, maize, and chick-peas.*

Varietal differences

The genetic control of micronutrient uptake and utilization is well documented, if not well understood, by results showing a wide range of efficiency within many crop species [10]. The genetic diversity of the world's crop plants has allowed great expansion in plant breeding activities in the last two decades. The national and international breeding programs have been very successful in developing varieties that have high yield potential, are disease and pest resistant, and respond well to fertilization, primarily nitrogen. The success of these breeding programs has provided hope that, at least to some extent, it is possible to modify the plant to fit in an unfavorable environment instead of trying to change the environment. Randhawa and Takkar [74] have listed the varieties of five cereals (wheat, barley, rice, maize, and sorghum); two pulses (chick-peas and black gram); and two oil seeds (Raya and sunflowers) that have been found tolerant to Zn and Fe deficiency and to Mn and B toxicity (Table 3). Research on improving the efficiency of a crop species by improving its ability to absorb and utilize micronutrients is still in its early stages of development but is expanding. The advances made in developing varieties capable of tolerating high Al, high acidity and toxicity or deficiency of some of the micronutrients have yielded results of practical significance.

Wheat

Wheat seems to be the most studied crop species relative to genetic differences in micronutrient responses. It has been reported [79] that susceptibility to Zn deficiencies among the Indian wheats was closely related to their relative efficiency in the utilization of soil Zn. There were significant differences in the time of appearance and intensity of Zn deficiency symptoms, amount of yield depression, and in tissue Zn concentration. The same authors further reported that tissue concentrations of Zn in cultivars ranged from 4.2 to 28.3 ppm under Zn deficiency conditions and the responses to Zn increased as the inefficiency of utilization of Zn increased. Randhawa and Takkar [74] presented a comparison of three wheat cultivars for their susceptibility to Zn deficiency when three different growth media were used (Table 4). The results show the profound influence that the environmental condition has on the plant's response to micronutrients.

One study [61] compared seven genotypes of wheat, one of barley, and one of oats for their sensitivity to suboptimal supplies of Cu and for their ability to recover from Cu deficiency when Cu was applied at defined stages of growth. The genotypes differed markedly. HALBRED wheat and Clipper barley was less sensitive to Cu deficiency than were the wheat cultivars GABO, GLAIVO, Pinnacle Chotelerma, UP301, Durambia, and the oat cultivar Avon. The author further concluded that genotypes with relatively higher yield potential were less sensitive to Cu deficiency than were those with lower yield potential. There was no apparent association between

Table 3. Varietal tolerance to micronutrient deficiency or excess [74]

Crop	Varieties tolerant to Zinc deficiency	Mn toxicity	B toxicity	Fe deficiency
Wheat (*Triticum aestivum*)	WG377 WL212 UP301	K816	WG357 Vijay	–
Barley (*Hordeum vulgare*)	PL26, 27, 40, 74, 76 RD103 DL40, 70 BG7 BH2 Vijay	–	Vijay Vijay + Jyoli +	K19 Kesri
Rice (*Oryza sativa*)	Sabarmati Ratna Anna Purna Chauvery Madhukar Balmagna Caloro CR10-113 CEB24 BR24 S10-13	– –	– –	MTU17 IE71444 IR1561-2283 Karuna –
Maize (*Zea mays*)	Ganga 2, 3, 4 JML22 T41, TW			
Sorghum (*Sorghum vulgare*)	2077 × 1151 Swarna			
Chick-peas (*Cicer arietinum*)	P6828 N59 S26 BR78			
Black gram (*Vigna mungo*)	T65, 55 Khargaon 3			
Raya (*Brassica juncea*)	T51 AL198			
Sunflower (*Helianthus annuus*)	Aranavisski NP15			

Table 4. Relative tolerance to zinc deficiency of the wheat cultivars [74]

Cultivar	Method of screening: Sand culture	Pot culture	Field
Kalyansona	H	M	L
WG357	L	M	H
WP301	L	H	–

H = high, L = low, M = medium

dwarfgrowth and sensitivity to Cu deficiency in wheat. Genotypes with higher grain protein content were potentially more susceptible to Cu deficiency than were those with lower grain protein content.

Generally wheat is more susceptible to Cu deficiency than rye [35]. Crosses between wheat and rye produce *Triticale* which maintains the desirable tolerance to low Cu availability of the parental rye variety. Studies suggest that the copper efficiency trait of rye is carried on a single chromosome and that it should be possible to transfer this trait from rye to wheat, producing Cu-efficient wheat cultivars. There is little doubt that there are genetic differences between cultivars for micronutrient efficiency, but also that these differences are modified by the environment. In wheat there has been a substantial amount of research identifying micronutrient-efficient varieties; however, the mechanism controlling this efficiency and the effects of environmental conditions remain little understood.

Sorghum

Sorghum seems particularly susceptible to Fe deficiency; thus, much of the work on cultivar differences in sorghum has been concentrated on this element. The Fe-efficient cultivars KSS and Pioneer B46 sorghum took up more Fe and contained less P than did the Fe-inefficient cultivar B line and Wheatland [8]. Similarly, it was observed that in Fe-deficient soils SC369-3-IJB sorghum developed Fe chlorosis, whereas NK212 remained green [11]. Under Cu-deficient conditions PS-2 developed apparent Cu-deficiency symptoms, characterized by high P accumulation in the lower leaves. These authors concluded that efficient uptake of P may not be advantageous under Fe- and Cu-deficiency conditions. Kanan [46] observed that the pH of the medium was reduced to 3.5 by the adventitious roots and not by the seminal roots of sorghum CSH5. In his view the signal from the chlorotic leaves was transmitted to adventitious roots which produced more reductants to make more Fe available.

The Zn and phosphorus uptake characteristics of a drought-resistant variety, M35, and a drought-susceptible variety, M47, have been compared [72]. There is little difference in uptake of Zn by the roots of the two varieties; however, M47 is much more efficient at transporting Zn to the shoot. It was also noted that Zn inhibits the uptake of P much less in the drought-resistant variety than in the drought-susceptible variety. This difference may facilitate the survival of M35 under water stress, which also reduces P availability.

Rice

In rice Zn deficiency is quite common; it has been identified by IRRI as the most important nutritional factor, after nitrogen and phosphorus, in limiting rice yields [14]. Giordano and Mortvedt [33] compared 12 rice varieties, some of which were developed in the tropics and others in the United States. A marked difference in their responses to low Zn availability was observed, with the shortest duration varieties having the least tolerance to Zn deficiency. In experiments at CIAT [15], the Colombian varieties, in general, were found to be more tolerant of low availability of Zn than were those developed at IRRI. However, recent IRRI varieties such as IR42 have proven very tolerant to Zn deficiency as well as many other stresses [42].

Varietal differences in Fe-stress tolerance have also been reported in rice. Shim and Vose [78] ranked the varieties Rebifun, SIAM 29, and Paldal in order of decreasing ability to absorb inorganic Fe. Pandey and Kannan [64] also found that varieties differ in their ability to absorb and translocate inorganic Fe, although this ability was not well correlated with Fe-stress tolerance in the field. They did find, however, that Fe uptake was inhibited by high Ca concentrations in stress-susceptible varieties but unaffected in the stress-tolerant varieties. They classified varieties Basmati, B63 (Basmati mutant), TR23, TR25, PVR1, AU1 (IR8 mutant), and IET144 as tolerant and IR8, Sona, B36 (Basmati mutant), and Jaya as susceptible to Fe stress.

Maize

Genetic variations in the efficiency of uptake and utilization of some micronutrients have also been observed in maize, although the nature of the uptake efficiency is not clear. An Fe-efficient line, WF9, produced H^+ ions and greater reducing conditions in the rhizosphere than did the Fe-inefficient line YS^1/YS^1 [21]. This seems like a plausible explanation for the differences in efficiency. However, when the two varieties were grown together, the Fe uptake and utilization of the inefficient line were not helped by the presence of the efficient line.

Several studies have shown differential responses of maize line to Zn. Shuman et al. [76] concluded that there is little evidence to support the hypothesis that hybrids are more efficient in absorbing soil Zn. In their opinion the differences in responses to Zn are dependent on biological processes involved in the utilization of absorbed Zn. When a Zn-efficient cultivar – Conico Composite – was compared with Pioneer 3369A, a cultivar susceptible to Zn deficiency, it was concluded that the Zn in the tissue of Concio was more biologically active [65]. In another study comparing an efficient and an inefficient cultivar, it was concluded that the inefficient variety translocated less Zn from the roots to the shoot, did not utilize shoot Zn as efficiently to produce dry matter, and accumulated imbalanced quantities of the nutrients P, Fe, and Mn which are known to be associated with Zn deficiency [20]. The low efficiency of translocation and utilization of absorbed Zn, especially when a large quantity of P is available, has been attributed to the immobilization of large amounts of Zn in the cell wall where it is not available for biological processes, which take place within the cell membrane [90].

Legumes

Research on the selection of soybean lines for tolerance to adverse soil environments has been done for many years in the United States. The research has demonstrated genetic diversity especially in Fe efficiency. One test of 10 soybean varieties showed that Forrest was the most Fe inefficient and Bragg the most Fe efficient [9]. These authors pointed out problems that developed in the midwestern part of the United States as a result of the introduction of some new varieties. Reports of Fe deficiency were not common for soybeans on some marginally low Fe soils while the variety Hawkeye was grown. When new higher yielding varieties were introduced, the incidence of Fe deficiency increased dramatically. This can be expected to occur in other parts of the world also since varieties are usually selected and developed on highly fertile soils without regard to their nutrient efficiency.

Some genetic diversity in micronutrient varietal responses has been reported in other food-grain legumes. Some varieties of Kabuli type (bold seeded) chick-peas are more susceptible to Fe deficiency than are others. In calcareous soils, Fe deficiency becomes visible after 6–8 weeks of seeding and may persist in highly susceptible varieties, even to the point of killing the plants. Sometimes Fe chlorosis reappears in some genotypes after irrigation or rainfall. Genotypic differences in Kabuli type chick-pea cultivars are being recorded at the International Center for Agricultural Research in the Dry Areas (ICARDA), and in a cooperative project between ICRISAT and ICARDA (personal communication from K. B. Singh, 1982) the cultivars tolerant to Fe deficiency have been identified. Likewise in groundnuts, differences in micronutrient sensitivity exist. It has been shown that the use of Fe-efficient groundnut varieties could save the cost of Fe fertilizer applications and still provide high yields [39]. Similar differences in Fe efficiency of dry beans have also been reported in the United States [25].

The genetic potential for improvement in micronutrient utilization in legumes other than soybeans has been exploited very little. There exists a wide variety of legume species and local varieties in the tropics. The collection, characterization, and utilization of this material in breeding programs is increasing and will provide a strong base for the selection of micronutrient-efficient varieties.

Roots and tubers – cassava and potatoes

Cassava is an important crop in the tropics, particularly on the acid infertile, aluminium-rich soils, where toxicity of Al and sometimes Mn is a major problem for most crops. Considerable genetic diversity has also been demonstrated within this crop. Large numbers of varieties of cassava have been screened for their acid tolerance. In a lime and micronutrient trial by CIAT in Colombia it was observed that liming reduced the uptake of Zn, Mn, Cu, and B [41]. High levels of liming greatly reduced yield by inducing Zn deficiency. Trials on the Zn-deficient soils of Punjab (India) [37] demonstrated differences in the responsiveness of potato varieties to Zn fertilizer applications. The varieties Kufri-Chandar-Mukhi and Kufri-Alankar were more responsive than were the varieties Kufri-Sandhuri and Kufri-Joti. The authors also noted a greater response to Zn in the winter than in the summer which indicated an interaction with climate.

Path of micronutrient uptake

In order to understand the dynamics of the micronutrient needs of tropical food crops, an explanation of the factors that control the rate of uptake and the timing of the needs is necessary. The various micronutrients have different mobility characteristics in the soil, and they are needed in widely differing quantities; in addition, the plants vary in their ability to redistribute the micronutrients from older tissue to new growing points or for grain filling. The mobility of nutrients in the soil and plant, the quantities of micronutrients in the seed, and environmental conditions all affect the quantity and timing of micronutrient needs and uptake.

The amount of uptake of micronutrients from the soil solution is dependent on several factors including (1) the rate and distance of movement of nutrients in the soil; (2) the volume of soil the plant is exploiting; and (3) the plant's capacity to absorb the nutrient [4]. Nutrients move to the plant root by diffusion and mass flow [3]. Diffusion occurs along a concentration gradient. As plant roots absorb nutrients, the soil environment near the root is depleted of the nutrient and the gradient is thus created. As long as root uptake exceeds the rate of movement of nutrients toward the root, diffusion will continue. The rate of diffusion of an ion depends on the physical characteristics of the ion, the soil's volumetric moisture content, soil texture, and reactions between the soil and the ion. Besides the innate differences in mobility of micronutrients in soil, the rate of movement of micronutrients is influenced by the plant's uptake characteristics. Plants that are very efficient at absorbing nutrients at low concentrations will speed diffusion by creating a large concentration gradient.

The other mode of micronutrient movement to the plant is by mass flow. The plant loses water to the atmosphere by transpiration, and this induces a flow of water to the root where it is absorbed. The water moving to the root has nutrients dissolved in it. Thus, the rate of supply of nutrients to the root is related to the plant's transpiration rate. Very high transpiration rates would increase the flow of nutrients to the root, and lower transpiration rates would decrease the nutrient flow. High transpiration rates occur with high temperature, low humidity, and high solar radiation, which are found throughout much of the arid and semiarid tropics as well as part of the humid tropics. This is an oversimplification, though, since soil moisture also limits transpiration. As low moisture decreases transpiration and increases the tortuosity of the diffusion path, nutrient mass flow and nutrient diffusion will both decrease.

Research on nutrient movement to roots indicates that Cu, Fe, and Mn *do not move in the soil to any great extent with mass flow [5, 63]*. Thus, nutrients only become available to the plant as the roots explore new volumes of soil and as the relatively slow diffusion process takes place. On the other hand, Mo moves freely by mass flow to the plant root.

Mycorrhizae may play a role in the uptake of these relatively immobile micronutrients. Vesicular-arbuscular mycorrhizae are fungi that infect the roots of most plant species. They have been shown to play a role in P uptake. Their hyphae extend out from the root into the soil and in so doing increase the volume of soil that the plant can deplete of nutrients that are very mobile. A study of mycorrhizae on cassava showed that elimination of the fungus caused about 10% decrease in Zn uptake [88]. Similarly, it was found that the presence of mycorrhizae increased Zn and Cu uptake in both maize and soybeans but had little effect on Mn uptake [51]. The role of mycorrhizae in micronutrient uptake has been studied very little, and the data are inconclusive to date.

The second factor influencing micronutrient availability is the volume of soil being exploited by the crop. The rooting pattern of crops grown in some tropical locations is quite different from that of crops growing in deep fertile soils. In particular, the high aluminium content of the subsoils in large areas of South America inhibits root penetration. As problems of water availability and adaptation of varieties to these environments progress, it is probable that the incidence of micronutrient deficiencies will increase.

A third factor is the plant's capacity to absorb and utilize the micronutrients that are available. The uptake process is best described by the membrane carrier site model. This model depicts sites located on the membrane which actively transport ions from outside the membrane to the cytoplasm. This process utilizes metabolic energy; thus, uptake is affected by temperature, water stress, and respiration-inhibiting chemicals. It seems that Zn, Cu, Mn, and B are absorbed by active uptake [6]. After studying the kinetics of the uptake of these four nutrients, Bowen also concluded that there are three separate uptake mechanisms operating. One actively transports B, another Mn, and the third both Cu and Zn. These two compete for the same uptake sites. Some earlier studies suggested that Zn uptake is passive, but Moore [59] pointed out that this conclusion is probably incorrect because of the way short-term, excised root experiments are often conducted.

The timing of the onset of micronutrient deficiency symptoms is influenced by the seed nutrient reserves and the plant's ability to redistribute nutrients from mature to growing tissue. According to Tiffin [85], seed reserves of micronutrients fall into three classes. The first includes only Mo, which is required in such small quantities that usually the seed contains an adequate amount to allow the plant to grow to maturity. The second group includes Cu and Zn. The seed reserves of these elements are adequate to delay the onset of deficiency, but without an adequate supply of available nutrients in the soil a deficiency is sure to occur. The third group includes B, Mn, and Fe. The seed reserves of these elements are so small that if soil is low in available nutrients deficiency symptoms will occur very soon after germination.

All of the micronutrients can move through the xylem tissue from the roots to the aerial portions of the plant. However, once in a leaf they differ in their ability to be redistributed to new expanding leaves or the filling grain. Boron is virtually immobile once it reaches a plant organ [85]. Thus, a continuous supply of B is needed by a crop to avoid deficiency. At the other extreme is molybdenum. Mo is readily redistributed via the phloem tissue to the other parts of the plant where it is needed [57]. The other micronutrients Zn, Cu, Fe, and Mn are intermediate in mobility. The deficiency symptoms of all four of these appear first in the youngest leaves. This suggests that the plant's ability to redistribute these micronutrients from mature to growing tissue is limited. It has been shown that in wheat Cu is essentially immobile until a leaf senescences [40]. At that point most of the Cu is redistributed to younger leaves or the grain. It is reported that in sorghum Cu and Zn were retranslocated from the vegetative tissue to the head but Mn was not [44]. In maize at least some Zn is redistributed from the vegetative tissue, mostly the stalk, to the grain [56]. Although some redistribution is evident, it is probable that a continuous supply of each micronutrient except Mo is needed to avoid deficiency and a reduction in yield.

Effects of climate

The two main components of climate affecting micronutrient availability are temperature and moisture availability. The effect of these factors has been studied most extensively in temperate regions; little work on their effects on tropical crops has been reported. Nevertheless, some general conclusions are still possible.

Zinc deficiency early in the growing season is often associated with cool soil temperatures. Sharma and Motiramani [77] reported that the response of rice to Zn applications decreased with an increase in soil temperature. Martin et al. [55] found that high levels of P induced Zn deficiency in cool weather but not in hot weather on soils low in available Zn. Lucas and Knezek [54] suggest that the combination of low light intensity and cool soil temperatures account for the observed greater incidence of Zn deficiency when the weather is wet and cloudy, and Chino and Baba [18] confirm that shading and low temperatures reduce Zn translocation to the plant tops. Lindsay [52] suggests that, in addition to changes in Zn transformations in the soil caused by cool temperature, reduced root development resulting in a less favourable shoot : root ratio may increase the incidence and severity of Zn deficiency. Randhawa and Nayyar [73] observed that in India micronutrient deficiencies are most severe in cold weather and mild or absent in warm weather on marginally deficient soils.

Soil moisture also affects micronutrient availability. Continuous submergence increases Zn deficiences in rice regardless of the soil pH [14, 81, 83], and the application of Zn fertilizers often produces a dramatic increase in grain yield. Similarly Gangwar and Mann [31] and Brar and Sekhon [7] reported greater responses to Zn applications in rice under flooded conditions than under nonflooded conditions.

Excess moisture increases the availability and uptake of Fe, Mo, and Mn [50]. The increased solubility of Fe caused by flooding may help rice crops, which seem to have a higher Fe requirement than do other crops. In fact, flooding can actually cause Fe toxicity on some soils [75].

Dry soil conditions can cause reduced micronutrient uptake, particularly among those that do not move through the soil by mass flow to the root. The ions of Cu, Fe, and Mn must move to the root by diffusion, as mentioned earlier, through the soil liquid phase. As the soil dries, the tortuosity of the diffusion path increases rapidly. Porter et al. [67] report that the rate of diffusion decreases 6- and 25-fold at 1 and 15 atmosphere of soil water potential, respectively. This, of course, reduces uptake substantially, especially when roots are not growing rapidly enough to exploit new volumes of soil. A more detailed review of the effects of climate on micronutrient availability is given by Lucas and Knezek [54]; however, the effects of climate on both micronutrient reactions in the soil and on crop uptake are not well understood especially under tropical conditions.

Crop management and yield levels

Besides the nature of the crop and its variety, crop management factors and the yield level also influence the frequency and severity of micronutrient deficiencies. The micronutrient removal per ton of dry matter produced by a crop is indicated in Table 5. The introduction of high-yielding varieties, the increased use of high-analysis NPK fertilizers, and increases in cropping intensity can all lead to micronutrient deficiency problems. The principal reason for the increase in deficiencies is the increased demand placed on the soil to supply nutrients for the increased crop yield and the increased number of crops per year. The soil's ability to supply the required quantities of micronutrients may have been adequate for centuries of traditional cropping and traditional low yields, but it is not adequate for high-intensity cropping and high yields.

Reports of micronutrient deficiency are increasing in number. Randhawa and Nayyar [73] reported that in India before 1966, when low-yielding and less-fertilizer-responsive varieties were used, only low-to-moderate responses to micronutrient applications were recorded on a few soils. However, since that time the frequency of responses to micronutrients, especially Zn, has

Table 5. Micronutrients removed by a crop in grams per ton of dry matter

	Fe	Mn	B	Zn	Cu	Mo	Source
Cereals							
Rice	61	270	6	16	7	2	[24]
Maize[a]	1200	320	–	130	130	–	[48]
Wheat	232	26	18	21	9	0.80	[29]
Sorghum	360	27	27	36	3	1.05	[29]
Pearl millet	264	23	27	22	9	0.84	[29]
Roots and Tubers							
Cassava	200	75	25	75	8	–	[2]
Potato	160	12	50	9	12	0.28	[29]
Pulses							
Mung beans	170	38	32	13	11	1.05	[29]
Chick-peas[a]	57	29	–	38	14	–	b
Pigeon peas[a]	39	14	–	23	13	–	b
Oil Seeds							
Groundnuts	499	39	44	9	5	1.32	[29]
Soybeans	242	147	–	52	69	–	[68]

[a]Grain only.
[b]Jambunathan, 1983, personal communication.

increased considerably. The mean and range of this response to Zn for a large number of crops are shown in Table 6. The increases in micronutrient responses have also been reviewed by Kanwar and Randhawa [47], Takkar and Randhawa [81], and Katyal and Sharma [48]. Summarizing the thousands of fertilizer response experiments on farmers' fields, these authors reported that 50%–60% of the sites showed a significant increase in grain yield due to Zn applications. In some districts the yield increase due to Zn was as high as 30%–40% with regard to the controls. The responses to several micronutrients in India are given in Table 7.

Table 6. Responses of crops to zinc application in field experiments conducted in India from 1967 to 1980 [73, 82]

	Number of experiments	Range of response (*min. & max.*) *in* individual field experiments	Range of *mean value of* responses in various states	Average *response* mean of all experiments
		(kg/ha)	(kg/ha)	(kg/ha)
Wheat	1,555	0.0–4,750	330–1,480	370
Rice	799	0.0–5,470	290–1,300	630
Maize	170	1.0–3,090	250–800	520
Pearl millet	207	1.0–670	170–180	150
Sorghum	134	40.0–1,350	180–520	340
Chick-peas	12	100.0–870	230–560	310
Groundnuts	61	50.0–1,210	180–470	410

Table 7. Yield increases of crops due to micronutrient applications other than zinc in India [73]

Nutrient	Wheat	Rice	Groundnuts
		(kg/ha) (mean)	
Fe	580	1,440	240
Mn	430	360	–
Cu	380	530	–
B	520	340	–
Mo	440	–	–

Reports from other regions of the world have not been so systematic. However, the worldwide trend of increasing both cropping intensity and yields means that the frequency and magnitude of response to micronutrient fertilizer applications are also increasing. Cottenie et al. [23] report that Zn and Cu deficiencies in the Alfisols and Ultisols of West Africa are common. In addition, these African soils are more likely to exhibit Zn and Mn deficiencies with liming and continuous cropping [45]. These are management practices that will become more common as the needs for local food production increase. Lopes [53], while reviewing soil micronutrients as constraints to crop production, concluded that Zn is seriously limited on the Campo-Cerrado soils of Brazil and the Llanos Orientalis in Colombia; B and Zn are limited on some Mollisols of Colombia; B, Cu, and Mo on some Vertisols of Peru; and Mo on some Andosols in Latin America. A survey of soil samples from the Campo-Cerrado region showed 95% below the critical level for Zn, 70% for Cu, and 37% for Mn. Lopes also reported dramatic crop response to Zn applications, in maize, sorghum, and soybeans. As row crops are introduced into new regions in Latin America and as the level of inputs increases in areas that are already in food crop production, the magnitude of the micronutrient deficiency problem will become clearer. On the basis of the limited data available, it seems very likely that the crop needs for micronutrients will exceed the soil's capacity to supply them throughout most of Latin America.

Continuous cropping and high use of fertilizers without adequate amounts of micronutrients also increase micronutrient deficiency. Prasad et al. [68] studied the effect of continous cropping and fertilizer use on the total uptake of micronutrients from the soil. As can be seen in Figure 2, the amounts of Cu, Zn, and Mn removed by four crops in a maize-wheat rotation increased dramatically with increasing rates of NPK applications. In this relatively short-term experiment no decline in soil micronutrient levels was detected as result of this high micronutrient demand. However, in some longer term experiments declines in soil micronutrients are evident. Subba Rao and Ghosh [80] showed that after 7 years of cropping in a pearl millet-wheat-cowpeas rotation, i.e., after harvesting 21 crops, the available Zn in the soil declined by 18.9%–30.6% for the nonfertilized and highest NPK

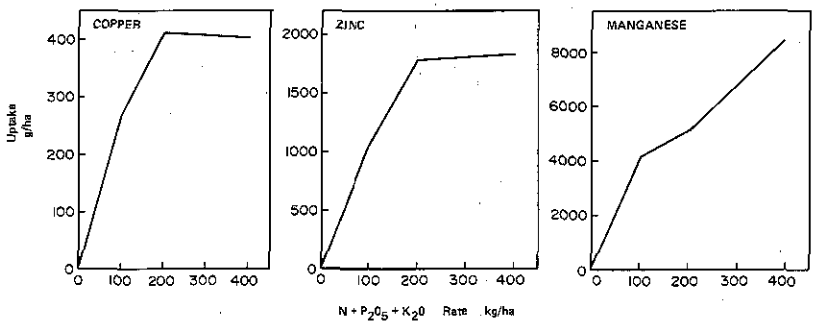

Figure 2. Increase in micronutrient uptake caused by use of N-P-K fertilizer

treatments, respectively. The annual removal of zinc ranged from 173 g/ha in the check to 358 g/ha in the highest NPK treatment. The authors also observed that inclusion of zinc with NPK treatment increased the zinc uptake still more. However, there was only a slight increase in available zinc in the soil due to the continous addition of Zn.

In India [69] it was observed that the changes in the available soil micronutrients took place after 8 years of continuous cropping in a soybean-potato-wheat rotation with various treatments of fertilizer, lime, and manure (Table 8). When farmyard manure was added, the available levels of Zn, Cu,

Table 8. Changes in available micronutrients in soil after 8 years of continuous cropping with a soybean-potato-wheat rotation

Treatment	Available micronutrients (ppm)			
	Zn	Cu	Fe	Mn
Initial value	1.11	2.00	47	57
After 8 years cropping				
No fertilizer	0.58	2.08	28	53
NPK	0.62	2.03	38	68
NPK + lime	0.61	1.98	21	30
NPK + farmyard manure (FYM)	1.29	2.54	54	84

Fe, and Mn all increased. In the other treatments the levels of Zn, Mn, and Fe were significantly reduced by the 8 years of cropping, especially in the NPK and lime treatment. The availability of Cu, however, was not much affected. The addition of FYM with NPK treatment increased all the micronutrients in the soil. This indicates that two ways of eliminating micronutrient deficiency are through the use of farmyard manure and through inclusion of a specific micronutrient fertilization schedule.

The use of NPK fertilizer clearly increases the crop demand for micronutrients. Fertilizer consumption in the tropics has been increasing at a rapid rate, particularly since 1976 (Figure 3). It is already evident that the incidence

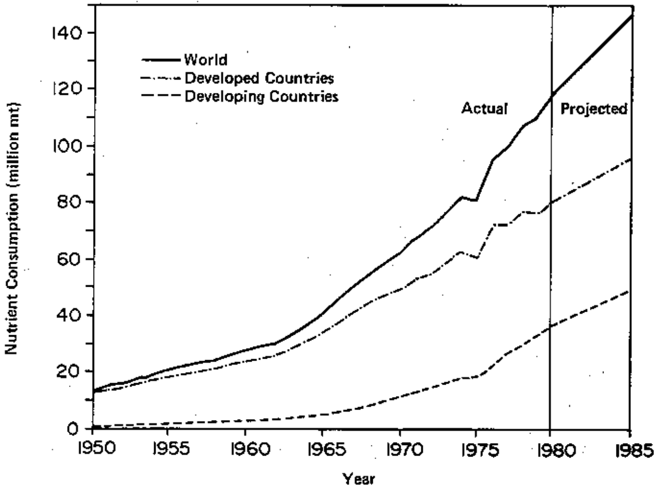

Figure 3. Evolution of total nutrient ($N + P_2O_5 + K_2O$) consumption [60]

of micronutrient deficiencies is increasing in some regions of the tropics. The consumption of NPK fertilizers, the adoption of high-yielding varieties and modern crop management, yield levels, and micronutrient deficiencies will probably all increase.

Micronutrient uptake, hence demand, by important tropical crops for producing the current average yields and the modest commercial or optimum yields are given in Table 9. It may be observed that the micronutrient needs increase in proportion to expected yield; hence, to meet this demand a corresponding input of micronutrients is necessary since the soil may not sustain an adequate supply for years of intensive cropping at high yield levels.

The amount of micronutrient fertilizer required to supply adequate nutrient levels will depend on many factors relating to crop, soil, cropping system, and management. The incidental addition of micronutrients as trace impurities in many fertilizers and irrigation water will be another source of their supply.

It may be concluded, however, that what was once satisfactory for traditional and subsistence agriculture will not remain satisfactory for modern agriculture based on the increased use of inputs required for high production levels. The micronutrient deficiency problems will grow in number and intensity and become more serious, first on those soils inherently deficient in the specific micronutrients, and later even on those soils that are presently marginal in micronutrient supply. These marginal soils will become more responsive because of a depletion of available micronutrients. A survey of world literature shows that Zn deficiency is the most serious micronutrient deficiency in the tropics, and it is becoming as important as deficiencies of N, P, K, S and Ca.

Table 9. Estimates of the current and projected rates of micronutrient removal rates if yields are increased

	Current yield		Micronutrient removal (g/ha)						Projected high yield level	Micronutrient removal (g/ha)					
	Economic	Total dry matter	Fe	Mn	B	Zn	Cu	Mo		Fe	Mn	B	Zn	Cu	Mo
	(mt/ha)		(g/ha)						(mt/ha)	(g/ha)					
Cereals															
Rice	2.2	5.5	336	1,485	33	88	39	4.4	6.0	915	4,000	90	240	110	12
Maize	1.5	3.7	1,800	480	–	195	195	–	5.0	6,000	1,600	–	650	650	–
Wheat	1.6	4.3	998	112	77	90	39	3.4	5.0	3,100	350	240	280	120	11
Sorghum	0.9	1.8	648	49	49	65	5	1.9	5.0	3,600	270	270	360	28	11
Pearl millet	0.6	1.2	102	12	–	24	5	–	4.0	680	80	–	160	33	–
Roots and tubers															
Cassava (fresh wt)	9.0	5.4	1,080	405	135	405	42	–	40	4,800	1,800	600	1,800	187	–
Potatoes (fresh wt)	10.6	–	1,700	127	530	95	127	3.0	30	4,800	360	1,500	270	360	9
Pulses															
Mung beans	0.5	1.5	255	57	48	20	17	1.6	3.0	1,530	340	290	120	100	10
Chick-peas	0.5	1.5	29	15	—	19	7	–	4.0	230	120	–	150	56	–
Pigeon peas	0.5	1.5	20	7	—	12	7	–	4.0	160	60	–	100	56	–
Oil seeds															
Groundnuts	0.8	2.4	1,200	94	106	22	12	2.9	5.0	7,500	590	660	140	75	18
Soybeans	1.6	4.8	1,160	706	–	250	331	–	4.0	3,600	2,200	–	780	1,000	–

Conclusions and their implications for further research

Micronutrient deficiency is becoming a constraint to crop production in the tropics. The tolerance of different cultivars to micronutrient deficiency can help in adapting crops and varieties to situations of specific micronutrient deficiency. Intensive research on screening of varieties that are resistant to micronutrient stress, and utilization of this information for breeding varieties having these characteristics deserve high priority. In addition to variety development, some specific research is required to increase our understanding of the micronutrient needs of tropical food crops. This research includes the following:

(1) Long-term studies on the depletion of micronutrients under intensive cropping with high-yielding varieties and moderate-to-heavy fertilizer input.
(2) Studies of the interaction of micronutrients with major fertilizer nutrients, especially N, P, and S, in the nutrition of tropical crops.
(3) Studies on the management of tropical soils and crops to maintain high availability of micronutrients.
(4) Studies to obtain quantitative data on micronutrient removal by different crops in the tropics.
(5) Studies on how the root systems of different crops and varieties affect micronutrient stress.

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