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PLANT ADAPTATION TO MINERAL STRESS IN PROBLEM SOILS [1]

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1. INTRODUCTION

Crop production ultimately depends upon interactions between plant genetic potentials and various stress factors of the environment. Until recently, plant genotype-mineral stress relationships have been largely ignored by research scientists, and particularly by research administrators.

In the past, our approach to soil fertility problems has emphasized «changing the soil to fit the plant.» As soil scientists, we have said to the plant breeder, «Give us a variety having climatic adaptation, insect and disease resistance, high yield and high quality, and we will adjust soil fertility factors to 'optimum' levels for the plant.» As a result of this approach, many crop varieties have been developed under nearly ideal conditions of soil fertility and pH. Such varieties are like «incubator babies.» They do well inside the incubator but may not be able to tolerate the stresses of the outside world. These varieties may develop mineral toxicity or deficiency when grown on soils that are only slightly different from those on which they were developed.

Examples of plants having adaptation limitations are as follows: The famous «Green Revolution» wheat varieties, like Sonora 63, developed in Mexico, will not tolerate the strongly acid, Al-toxic soils of Brazil. In the United States the wheat variety «Gaines,» which still holds the world yield record of 209 bushels per acre, in the State of Washington, is also extremely sensitive to Al (This explains why this variety does poorly when moved from the Palouse soils, on which it was developed,

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to adjacent soils that are slightly more acidic). Wheat varieties developed at Wooster, Ohio, are generally more tolerant to acid, Al-toxic, soils than those developed in the adjacent state of Indiana. The «Green Revolution» rice variety «IR-8» is much more sensitive to Fe toxicity than native varieties of Southeast Asia. «Wayne» soybean, selected for high yield (80 bushels per acre), shows Fe-deficiency chlorosis on certain calcareous soils of the Mid-western United States. Some corn and tomato inbred lines cannot absorb and/or use Fe efficiently, even in acid soils at pH 5.0, or below. One corn inbred line could not obtain adequate Mo from a strongly acid, normally Al-toxic soil and, hence, was more limited by Mo deficiency than by Al toxicity. (See references *13, 14, 15*).

The practice of fertilizing and liming the soil to «optimum» levels has been profitable on the moderately acid soils of the United States where fertilizers, lime and fuel were relatively cheap. However, in many parts of the world, this approach has never been very practical, and it is even less so today than formerly. Even in the «developed» countries of the world, our concern with conservation of energy and other resources and with environmental pollution are causing some re-examination of former agricultural practices. But the fact remains that in both «developing» and «developed» countries, some soil conditions are simply not economically correctable with current technology. There is a growing feeling that we should seek greater «accommodations» with «nature» rather than always trying to «bend» her to our own will. For example, in some parts of the Tropics, where food and energy shortages are most acute, there is developing among scientists, the idea of using a «minimum input,» rather than a «maxium output», agriculture for marginal soils. In such cases, tailoring the plant more precisely to fit the soil may be more economical, at least in the short run, (but may be also in the long run), than attempting to change the soil to fit the most exacting plant. Native farmers in areas of marginal soils have always had to live with a «minimum input» system. The application of «high input» technology to such situations is often not only unprofitable, but harmful.

2. SOIL PROBLEMS AMENABLE TO A PLANT SELECTION OR BREEDING APPROACH

Soil situations in which a plant selection or breeding approach seems promising are as follows: acid, Al-toxic subsoils that are difficult to lime; strongly acid mine spoils where rapid plant cover and soil stabilization are desired at minimum cost; steep pasture lands that are strongly acid, infertile and difficult to lime, even in the surface soil layer; vast areas of strongly acid, P-fixing surface soils and subsoils of the tropics (Campo Cerrado of Brazil, occupying 20% of that country, and the Llanos, in eastern Colombia); saline soils; soils polluted with heavy metals; calcareous soils having Fe unavailability or other micronutrient problems; wet soils; dry soils; and, even perhaps, hard soils.

A plant selection and breeding approach is also needed for improving the efficiencies of fertilizers, particularly P and N, on our «good» soils. For example, the use of N-efficient genotypes would save energy, make better use of limited fertilizer supplies, and reduce the dangers of groundwater pollution. Phosphorus-efficient genotypes are needed, along with cheaper P fertilizers that are less subject to fixation.

Plant breeding can also be used to regulate the mineral composition as well as the yield of crops, and thereby to improve the quality of food for both people and livestock. For example, we need forages that will accumulate sufficient Mg to prevent grass tetany in animals that graze exclusively on these plants (*1*). We may want plants that exclude Cd, an element which accumulates in man over a lifetime (*14*).

3. STEPS IN A PLANT GENETIC APPROACH

1. Select a stress tolerant species (Weeping lovegrass instead of alfalfa on acid mine spoils).
2. Select the most tolerant cultivar within a species (Bluegrass varieties differ by 25 fold in their tolerances to an acid, Al-toxic soil).
3. Select and propagate the most tolerant individual plant within an established cultivar. (The acid soil (Al) tolerance of tall fescue has been increased 40% in one cycle of recurrent selection-Jack Murray, Beltsville). Such differences between individual plants of «uniform» varieties appear only when stress is applied.
4. Breed for various combinations of desirable traits.

Many problems of plant adaptation to «problem» soils can be solved by application of steps 1,2 and 3, without the use of complicated breeding procedures.

4. BENEFITS OF A PLANT GENETIC APPROACH TO SOIL PROBLEMS

A plant selection or breeding approach to soil fertility problems has several advantages. It is «ecologically clean,» energy conserving and often cheaper than trying to modify the soil to fit the most demanding plant. The approach is thus compatible with our national and international goals of economical food production, conservation of fertilizers and energy, and control of pollution. This approach is especially appropriate for countries having little foreign exchange.

More specific benefits of the plant genetic approach are as follows:

1. Increased yields of crop species grown on present acreage (Introduction or creation of a variety more specifically adapted to prevailing stresses)-selection of an Fe-efficient strain of weeping lovegrass for calcareous soils (*35*)).
2. Expansion of crop acreage of a species to marginal soils not presently suited to the crop (Extension of wheat acreage into Campo Cerrado of Brazil by the use of Al-tolerant varieties).
3. Introduction of new and more profitable species for specific needs (Introduction of an Al-tolerant, cold tolerant strain of limpograss for use on strongly acid, high altitude mine spoils or on acid sites in more northern climates (*29*)).
4. Crop improvement through the gradual introduction of crops having more exacting growth requirements and greater value. (For example, on an acid mine spoil site, one could begin with Al-tolerant weeping lovegrass and end with Al-sensitive barley or alfalfa, according to prevailing economic and other constraints).

5. OBJECTIONS TO THE PLANT GENETIC APPROACH

a. *Aluminum tolerant plants may be lower yielding* in the absence of Al (limed soils). This is not necessarily true in crop plants that have been studied. A high degree of Al tolerance has been found in snapbean, cotton, tomato, wheat and barley varieties that also produce high yields in the absence of Al. But even if some yield potential is sacrificed in acquiring Al tolerance, the result may still be profitable because lower levels of lime and P would probably be required for a given yield of a given quality crop.

b. *Some Al-tolerant wheat varieties are tall-strawed and, hence, may lodge under high fertilization.* (Carlos Camargo, at Oregon State (*2*), has recently found a source of Al tolerance in the short-strawed, high yielding wheats and has suggested genetic methods for making use of this trait).

c. *Crop quality (mineral content) may be lowered.* This is not necessarily true. For example, BH 1146 wheat (Al tolerant) is more Mg efficient than Al--sensitive Sonora 63. There is also evidence that Al tolerant plants are more efficient in absorbing Ca and P at low concentrations in the growth medium.

d. *The use of lime and fertilizer may be discouraged.*
Just the opposite may occur because the use of the genetic approach will promote the use of marginal land which previously received no treatment. The proposed approach does not mean the abolition of lime and fertilizer use. Instead, it advocates more effective use of plant genetic diversity in solving the more difficult problems of soil fertility. Inputs of lime and fertilizer would still be required but at lower levels than those used in intensive agriculture.

e. *Soil will be impoverished.*
The approach does not propose the bleeding of soil fertility to zero levels. Instead, it promotes more effective use of fertilizers already fixed by the soil and of those added as amendments. The idea is to produce profitable yields of acceptable quality with lower inputs per unit of output.

f. *Breeding for high levels of Al-tolerance may increase vulnerability to other stresses.*
This is a valid concern. Certain trade-offs may be necessary. The whole approach must be applied within a framework of prevailing economic and other constraints.

g. *In tailoring the plant to fit the soil, theoretically, endless plant-genotype-soil «prescriptions» would be required.*
It is true that there is a practical limit in formulating plant genotype-soil combinations. However, the principle can be used to produce better management «packages» than we have at present. For example, if one decides to grow wheat in the Cerrado of Brazil, he would grow BH 1146, instead of Sonora 63, and he would require perhaps half as much lime and phosphate fertilizer as he would need with Sonora 63 to produce a profitable yield of acceptable quality.

6. OBJECTIVES OF MINERAL STRESS RESEARCH (PLANT STRESS LABORATORY AT BELTSVILLE)

1. Identify both present and potential mineral stress factors in problem soils.

2. Screen plant germplasm for stress tolerance.

3. Collaborate with plant breeders in developing superior genotypes for specific problem soils.

4. Determine the physiological mechanisms of differential plant adaptation to mineral stress.

5. Use plant physiological traits to refine screening procedures and improve soil-plant management practices.

6. Use plant genotypes as indicators of potential mineral stress problems, in conjunction with conventional soil testing procedures.

7. Determine interactions between mineral stress and other environmental factors such as water, herbicides, temperature, pathogens, rhizobia and mycorrhiza.

7. THE ACID SOIL «INFERTILITY» COMPLEX

Soil acidity is still a major growth limiting factor in many parts of the world. Acid soil injury (particularly Al toxicity) is a very insidious problem; it may reduce fertilizer and water efficiency of plants and may often be mistaken for ordinary nutrient deficiency, drought, herbicide injury, low temperature damage, or even a plant disease. Aluminum toxicity in subsoils is particularly harmful because it causes shallow rooting, drought susceptibility and poor use of subsoil nutrients.

Acid soil toxicity is not a single factor, but rather, a complex of factors that may affect the growth of different plants through different physiological pathways, probably controlled by different genes. Furthermore, different acid soils having the same pH may cause different mineral stress problems in a given plant genotype.

Specific causes of poor plant growth on acid soils may vary with soil pH, clay mineral types and amounts, organic matter contents and kinds, levels of salts, and particularly with plant species or genotype. Growth limiting factors that have been associated with the acid soil «infertility» complex include toxicities of Al, Mn, and other metal ions; low pH *per se* (H^+ toxicity); and, deficiencies or unavailabilities of certain essential elements, particularly Ca, P, Mg and Mo. Even Fe deficiency has been reported in upland rice on acid soils of pH 5.1 to 5.8. In acid coal mine spoils and soils polluted with industrial wastes, Zn, Cu, Cd, Ni or Pb may be toxic to some plants. Acid soil factors may act somewhat independently, or more often together, to affect the growth of higher plants. They may also promote or inhibit the survival and function of rhizobia, mycorrhiza and other soil microflora.

At a soil pH above about 4.2, the H ion (pH *per se*) probably does not directly limit the growth of most crop plants. The detrimental effects of soil acidity are largely indirect. However, low pH, *per se*, can increase the Ca requirement of plants in a growth medium and may also restrict the growth of rhizobia or other soil microflora. In general, only the most sandy and highly leached (low CEC) acid soils are absolutely deficient in Ca or Mg for higher plants, but the rhizobia of certain legumes require higher Ca levels than do their host plants. In addition, excess Al or other elements may interfere with plant uptake and use of Ca, Mg, P or other essential elements. Unlike other micronutrients, Mo is more available in limed soils than in strongly acid soils. Hence, liming usually prevents deficiency, but some soils (Australia) may be absolutely low in Mo and require treatment for growing legumes.

Aluminum and Mn toxicities are the most prominent growth limiting factors in many acid soils. Aluminum toxicity is particularly severe below a soil pH of 5.0 but may occur as high as pH 5.5 in kaolinitic soils. Within this pH range, the clay minerals, which are aluminosilicates, become unstable, and some Al previously bound within the clay crystal structure moves to exchangeable positions on clay surfaces. Thus, in strongly acid soils the clay surfaces are primarily saturated with exchangeable Al ions and not H ions as previously supposed. Some of the Al released from structural positions goes into solution where it reacts with water to produce H ions which lower pH and keep it low. Much of the poor root development (and drought susceptibility) seen in acid (pH 5.0) subsoil layers is believed to be due primarily to Al toxicity which limits both rooting depth and degree of branching.

Manganese toxicity generally occurs in soils with pH values of 5.5 or below, if the soil parent materials contain sufficient total Mn. However, it can also occur at higher pH values (6.0, or above) in poorly drained or compacted soils where reducing conditions favor the production of divalent Mn which is most available for plant uptake. Thus, Mn toxicity can occur at pH values that are too high for Al toxicity. Soils of the Atlantic Coastal Plain of the United States are lower in total Mn than those of the Gulf Coastal Plain. Hence, at a given low pH, Mn toxicity is less likely in the former than in the latter.

8. DIFFERENTIAL PLANT TOLERANCES TO MINERAL STRESS

Plant species and varieties within species differ widely in tolerance to mineral stress of toxicity or difficiency. The individual publications that document these findings are too numerous to cite here, but the review papers listed will serve as an introduction to the literature. Pertinent references are numbers *5, 7, 8, 12, 13, 14, 15, 16, 17, 18, 24, 27, 33, 34, 36, 37*.

9. GENETIC CONTROL OF MINERAL STRESS TOLERANCE

Aluminum tolerance in certain barley populations is controlled by one major, dominant gene (*32*). In wheat, two and possibly three major, dominant genes, plus modifiers, are believed to be involved (*4, 23*). In corn Al tolerance appears to be qualitatively inherited (*32*). A single locus with a multiple allelic series has been postulated. Manganese tolerance in lettuce is reportedly controlled by one to four genes, depending upon the species (*14*). Iron efficiency in sorghum appears to be dominant or over-dominant (*10*).

10. PLANT GERMPLASM RELEASE

Considerable progress is being made in selecting and/or breeding plants for tolerance to mineral stress. Examples are as follows: Two sorghum varieties having superior Al and drought tolerance have been released for use on the Campo Cerrado soils of Brazil (Robert Schaffert, EMBRAPA/CNPMS, Sete Lagoas, MG, Brazil). In 1981, Duncan, of the Georgia Experiment Station in the United States, released an acid soil tolerant sorghum germplasm population (GPIR) (*9*). Lafever, of the Ohio Experiment Station at Wooster, released «Titan» wheat for use in eastern Ohio, where Al toxicity is a problem in acid subsoils (*3, 21, 22*). «Titan» is not as tolerant to Al as the Brazilian wheats, like BH 1146, but it is much more tolerant than Indiana varieties like Abe, Arthur and Redcoat, or Green Revolution varieties like Sonora 63. In 1980, Reid *et al.* (*31*) (USDA, Tucson, Arizona) released an Al-tolerant barley population for experimental purposes. This composite cross contains sources of Al tolerance from a world collection of germplasm. Fehr and Cianzio (*11*) registered AP9 (SI) C2 soybean germplasm (Reg. 200 GP *33*) in Iowa. This is a genetically diverse population with superior resistance to Fe deficiency chlorosis on calcareous soils.

11. PHYSIOLOGY OF PLANT ADAPTATION TO MINERAL STRESS

Aluminum tolerance has been variously associated with pH changes in root zones, Al trapping in non-metabolic sites, P efficiency, Ca and Mg uptake and transport, root CEC, root phosphatase activity, internal levels of Si, $NH4^{+}-NO_3$ tolerance or preference, organic acid content, Fe efficiency, and resistance to drought. For details see review references *7, 13, 14, 15, 24, 33, 36*.

Several more recent papers dealing with the physiology and biochemistry of Al injury are worthy of note. Naidoo (*28*) attributed the superior Al tolerance of Dade snapbean (compared with Romano) to a greater ability to tolerate a given level of Al within root cell nuclei. McLean and Rasmussen (*26*) found that Al caused an abnormal distribution of ribosomes on the endoplasmic reticulum of barley root cells. Interference in protein synthesis was postulated. Matsumoto *et al.* (*25*) found that Al was bound to P in DNA and not to the histone protein associated with the DNA double helix. For recent evidence concerning the distribution of Al in plants, see Huett and Menary (*19, 20*).

Manganese tolerance in plants has been associated with oxidizing powers of roots, Mn-absorption and transport rate, Mn entrapment in non-metabolic centers, high internal tolerance to Mn and the uptake and distribution of Si and Fe (*14*).

The weeping lovegrass strain FQ 22 is much more resistant to Fe-related chlorosis in calcareous soil and to low Fe concentrations in nutrient solution than is strain FQ 71 (*16*). Superior Fe efficiency in the FQ 22 strain has been associated with the ability to maintain a low pH in its root zone (which prevents Fe precipitation), a greater affinity for NH_4^+ –N vs NO_3^- –N, more effective transport of Fe from roots to tops, and restricted transport of Mn and Ca. Excesses of Mn and Ca may interfere with the metabolism of transported Fe in the chlorosis-susceptible FQ 71 genotype.

In tomatoes, Fe efficiency has been associated with a lowering of pH in the root zone and the release of a «reductant» which converts Fe^{3+} to Fe^{2+}, which is more available to plants. The principal «reductant» is believed to be caffeic acid or its derivatives (*30*).

12. CONCLUSIONS

Mineral stress in problem soils is not always economically correctable with current technology. An alternative or supplemental approach is to fit plants more precisely to soils. This approach does not propose the elimination of lime and fertilizers or the bleeding of soil fertility to zero levels. Instead, it advocates a more effective use of plant genetic diversity in solving some of the more difficult problems of soil fertility. The result will be plant genotype-soil-fertilizer-lime combinations that may be superior to medical «prescriptions» for people. The proposed approach involves the identification of present and potential growth limiting factors in problem soils, screening of available germplasm for tolerance, and the selection or breeding of superior cultivars for specific purposes. Such multi-disciplinary research, which is already in progress at several research centers, has a tremendous potential for alleviating present and anticipated food shortages throughout the World (*6*).

13. RESUMO

As tensões minerais existentes em muitos solos nem sempre são economicamente eliminadas pelo uso de tecnologias tradicionais. Uma alternativa suplementar seria a obtenção de plantas mais adequadas para esses solos. Não se propõe, aqui, a eliminação da calagem, ou da fertilização, ou o esgotamento da fertilidade natural do solo até zero, mas a utilização mais eficiente da diversidade genética das plantas na solução dos problemas mais difíceis da fertilidade dos solos. Desse modo, poder-se-ão obter combinações entre o genótipo da planta, o solo, a fertilização e a calagem superiores às recomendações agronômicas tradicionais. O esquema proposto envol-

ve a identificação dos fatores, atuais e potenciais, que limitam o crescimento nos solos-problema, a seleção do germoplasma disponível para a tolerância e o melhoramento, visando à obtenção de cultivares superiores para propósitos específicos. Tal pesquisa multidisciplinar, já em andamento em diversos centros de pesquisa, apresenta grande potencial para eliminar a carência, presente e futura, de alimentos no mundo.

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