ROLE OF THE RHIZOSPHERE IN IRON NUTRITION
OF PLANTS
(Invitational Paper)

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In neutral or alkaline soils, the availability of Fe to plants is extremely low and on these soils Fe deficiency is widespread. The maintenance of sufficient Fe supply for crop plants often makes it necessary to supply additional Fe in the form of Fe chelates to the soil or as leaf spray. Iron chelates are, however, rather expensive and in the long run efforts have to be made to increase the Fe availability in the soil or to pay more attention to selection and breeding of crop plants with high ability for Fe uptake; i.e. with high Fe-efficiency.

Iron deficiency in calcareous soils — lime chlorosis — is already a classical problem of plant physiology and ecology. The sensitivity of higher plants to lime chlorosis varies greatly among natural vegetation, different species of crop plants and even varieties within the same species.

Different sensitivity of crop plants to Fe chlorosis on calcareous soils can often be observed. A good example is in mixed cropping of fruit trees and annual species, where the fruit trees often show severe Fe chlorosis, whereas the annual species are the normal green colour. It is necessary to stress that the demand of different plant species for Fe as a plant nutrient is practically the same calculated per unit dry matter production. Iron efficiency must, therefore, be based on a special ability of the roots of some plants to take up sufficient Fe from a soil on which iron-inefficient plants show iron chlorosis.

With respect to the quantity of Fe necessary for normal plant growth, it is necessary to realize that the demand for Fe as a micronutrient is rather low (approx 1 kg Fe/ha per year for a crop of corn or wheat). This is a very low amount compared to the total Fe content ($\approx$60 tons Fe/ha per 15 cm) of a mineral soil.

Certainly from this total amount of Fe, a high proportion is incorporated in the primary minerals or clay minerals and only a small proportion is exposed to the surface or cover surfaces of clay minerals as Fe oxides or hydroxides. Nevertheless, the surface active portion of Fe is still rather high compared to the demand of the plants. The limiting factor in Fe nutrition on soils with a higher pH is therefore not the amount but the solubility of Fe. The solubility product of inorganic Fe is determined by the H^+ concentration; i.e. the pH of the soil, and the soil solution, respectively, and in addition to this by the redox potential (E_h); this determines the equilibrium of $Fe^{3+} \rightleftharpoons Fe^{2+}$ and the solubility of Fe^{2+} is several times higher than that of Fe^{3+} (Table 1).

Considering this equilibrium, in well-aerated soils of a high pH, the solubility of inorganic Fe will be far too low to cover the demand for Fe of crop plants. In this

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Table 1.   Content and solubility of iron in mineral soils

Redox potential (mV)	pH	$Fe(OH)_2$, (mg/l)	$Fe(OH)_3$, (mg/l)
+ 600	6	1.7×10^{-13}	1.7×10^{-14}
	5	1.7×10^{-11}	1.7×10^{-11}
+ 200	6	2.3	

In soil solution ($\approx 10^6$ l H_2O/ha) at 10^{-13} mg Fe^{2+}/litre = 10^{-7} mg Fe^{2+}/ha. Demand ≈ 10 g Fe/day per ha.

calculation, however, the possible contribution of organic compounds which may form chelates with the inorganic Fe and so shift the equilibrium towards higher amounts of soluble and available Fe, is not included. It has been demonstrated by Hodgson [13] and Geering *et al.* [12] that in soils with a higher content of organic substances and with a high microbial activity, at least other micronutrients like Mn, Zn and Cu are present in the soil solution in proportions similar to that of metal chelates. For Fe, unfortunately, no such data are available. It can be assumed, however, that in soils with higher amounts of organic matter and pH, the formation of Fe chelates may substantially contribute to the Fe nutrition of the plants. In soils low in organic matter, the contribution of these soil-born chelates for the Fe nutrition of the plants should, however, not be overestimated.

A further point to be considered is in relation to soil organic matter and Fe availability and Fe chlorosis. All factors which increase the HCO_3^- concentration in the soil solution and lead to increased HCO_3^- uptake are potentially chlorose-inducing [5], as HCO_3^- in the roots decreases via certain metabolic steps or Fe translocation into the shoot. The mechanism for this HCO_3^- action is not yet clear, although the effect is nevertheless quite obvious.

To increase the Fe availability to the plants on soils with a high pH, efforts to increase the pH by elementary sulfur or to decrease the redox potential are certainly possible, although rather difficult. With respect to the pH, this has been demonstrated by Kashirad and Bazargani [16] and Kashirad [15] in the Shiraz area on a calcareous soil, pH 8.3. Amounts of elementary sulfur up to 6000 kg/ha were necessary to decrease the pH from 8.3 to 7.6. This demonstrates that the amounts of sulfur needed to decrease the pH under these conditions (high content of $CaCO_3$) are far too high to be economical. It is known, however, that with various commercial fertilizers it is possible to change the soil pH slowly but substantially in long-term experiments, especially on soils with a lower buffering capacity. But even in soils with a high buffering capacity, this pH effect of fertilizer salts is detectable within a short time in the immediate vicinity of the roots — the rhizosphere. This has been demonstrated by Riley and Barber [22] with soybean supplied with different fertilizers (Table 2). Due to the preferential uptake of the anion from $Ca(NO_3)_2$, compared to the cation and preferential cation uptake from $(NH_4)_2SO_4$ compared to the anion, the pH in the soil and at the root surface in particular is decreased in the case of $(NH_4)_2SO_4$ and increased in the case of $Ca(NO_3)_2$ supply. Although this method of mechanical separation of the soil and the determination of the pH in the rhizosphere is rather crude, the tendency is clearly reflected, and at the

root surface, during the uptake process, the pH changes can be assumed to be much higher than those in Table 2.

Table 2. Effect of N fertilizer supplied as $(NH_4)_2SO_4$ and $Ca(NO_3)_2$ on the pH in the rhizosphere of soybean*

| Rhizosphere pH (without fertilizer, without plants) | pH in the soil | | | |
| | Bulk soil (outside of the rhizosphere) | | Within the rhizosphere | |
	NH_4-N	NO_3-N	NH_4-N	NO_3-N
5.2	4.98	5.43	4.71	6.60
6.3	5.90	7.00	5.60	7.05
6.7	6.64	7.01	6.25	7.19

*After Riley and Barber [22]. Duration of the experiment, 3 weeks.

A different pH at the root surface according to the N source must also affect the solubility of other plant nutrients, Fe in particular. NH_4 fertilizer should, therefore, have a positive effect and NO_3 fertilizer a negative one on Fe uptake. This was demonstrated by Farrahi-Aschtiani [11] in a pot experiment with a calcareous soil (Table 3). Compared to the unfertilized control, $Ca(NO_3)_2$ depressed shoot growth and induced Fe chlorosis, whereas $(NH_4)_2SO_4$ increased both chlorophyll content and shoot growth. This effect of Fe nutrition by the type of N fertilizer is certainly the reflection of the pH changes within the rhizosphere induced by different cation/anion uptake.

Table 3. Effect of 2 g N per pot as NH_4^+ or NO_3^- on chlorophyll content and growth of *Vinca minor* on a calcareous soil of pH 8.3*

Treatment	Chlorophyll content in the dry matter, relative values	Dry matter production per 100 plants, relative values
Control	100	100
$Ca(NO_3)_2$	69	39
$(NH_4)_2SO_4$	177	260

*After Farrahi-Aschtiani [11].

The conditions in the rhizosphere are also different in other respects compared to the bulk soil. Roots not only take up ions from the soil but also release quite considerable amounts not only of HCO_3^- and H^+ by respiration, but also organic compounds such as sugars, organic acids, amino acids and higher molecular compounds, like polysaccharides and polyuronic acids. This release of organic compounds is easy to demonstrate, particularly in the area of the root tip. Working under non-sterile conditions, the detection and identification of these root exudates are difficult, as these organic compounds are decomposed by microorganisms living in the rhizosphere and at the root surface. These root exudates, together with organic material from decaying root-cap cells and root hairs are the reason for the well-known high density of microorganisms in the rhizosphere compared to the bulk soil.

Table 4.   Release of organic substances (root exudates) from barley roots to the surrounding substrate under sterile conditions

Character	Nutrient solution	Solid substrate (glass ballotini)	
		3 mm	1 mm
Shoot DM/plant, g	57.3	50.7	52.7
Root, DM/plant, g	31.8	32.9	36.4
"Root exudates" in % of root DM	5.0	7.7	9.0

*After Barber and Gunn [3]. Duration of the experiment, 3 weeks.

The total amount of root exudates is rather high and is influenced by several factors such as mineral nutrition of the plant and mechanical resistance of the root substrate. Under sterile conditions, Barber and Gunn [3] demonstrated (Table 4) that, compared to the nutrient solution in a solid substrate, the exudation rate was higher in the one with small particle size, i.e. higher mechanical impedance in particular and that this exudate amounted to up to 9% of the root weight within 3 weeks. These root exudates themselves are rather effective in the solubilization of compounds of low solubility such as Fe phosphate (Table 5).

Table 5.   Dissolution of Fe^{II} phosphate (Vivianite) by rhizosphere products of *Sinapis alba* grown for three weeks under sterile conditions*

	Fe, μg/ml	P, μg/ml
Control (without addition)	0.7	0.7
Organic acid fraction	2.2	1.6
Amino acid fraction	7.3	3.5

*After Scheffer *et al.* [23].

Under non-sterile conditions, these organic root exudates are responsible for the high microbial activity in the rhizosphere. This high microbial activity affects directly or indirectly affects the E_h, pH and mineral element concentration within the rhizosphere. These factors combined can finally improve the mineral nutrition in the case of trace elements in particular, as has been demonstrated by Barber and Lee [4] with Fe and Zn. Even with a supply of Fe chelates, the microorganisms in the rhizosphere accelerated uptake and translocation of Fe to the shoots.

The mechanism by which these rhizosphere microorganisms can accelerate Fe uptake is not yet fully understood. There are, however, good indications that the redox potential is one of the main factors involved. High microbial activity in the rhizosphere simultaneously means a high demand of O_2. The O_2 supply can soon become a limiting factor and this will lead to a drop in the redox potential in the rhizosphere. In model experiments, this could be demonstrated by Trolldenier [24, 25] with rice and wheat. In

these experiments, it could further be shown that an insufficient supply of other nutrients can increase the root exudation rate, increase the microbial activity and finally decrease the redox potential in the substrate.

Table 6. Influence of potassium supply to rice on number of bacteria and concentration of O_2 and Fe^{2+} in the nutrient solution*

Treatment	Number of bacteria $\times 10^6$	Concentration in the nutrient solution	
		mg O_2/l	mg Fe^{2+}/l
K_2	1244	17.5	1.0
K_1	1686	8.6	2.4
K_2/K_0†	2036	0.5	10.6

*After Trolldenier [25].
†55 days K_2 and then 21 days K_0.

Potassium deficiency in particular increases the exudation rate and number of bacteria (Table 6). This in turn leads to the decrease in oxygen concentration and redox potential. With respect to the Fe nutrition, this drop in redox potential shifts the equilibrium from Fe^{3+} to Fe^{2+} and this will certainly increase the Fe uptake of the plants as Fe^{2+} is the main form of Fe taken up and transported in the shoot. All these changes in pH, E_h and formation of microbial products with chelating properties for Fe can take place in the rhizosphere and will certainly improve the Fe nutrition of plants even on soils with a high pH. It is obvious that plant species and varieties or ecotypes differ in their ability to change the conditions in the rhizosphere towards increased mobilization, and this might be one of the main reasons for differences in Fe-efficiency.
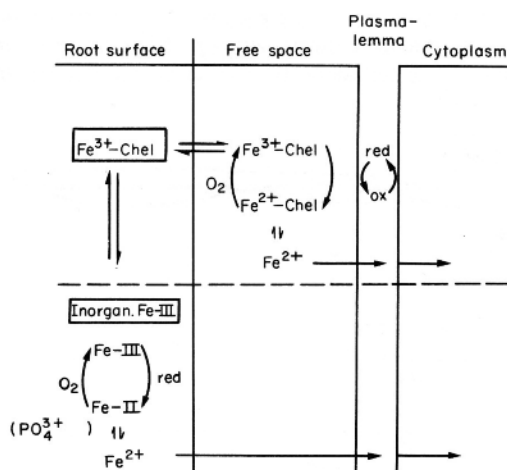
Fig. 1. Model for iron uptake by plant roots. Modified from Chaney *et al.* [9].

In order to understand better the complex term "Fe-efficiency" and the mechanism of Fe uptake, a few years ago we began some experiments in water culture with different plant species and different sources of Fe, chelates as well as inorganic Fe. There have already been a great number of reports on the relationships between Fe uptake, genotypical characterizations, species, varieties and Fe-efficiency [1, 7, 8, 28]. In nearly all the reports, however, Fe chelates like FeEDTA or FeEDDHA have been used as a source of Fe. For these chelates, the root surface is no diffusion barrier and the chelates can enter the free space of the roots. Therefore, all cells of the cortex can take up Fe from the chelates (Fig. 1). With inorganic Fe-III, however, the Fe is practically exclusively present in insoluble form as particles which can get in close contact with the root surface, but cannot enter the free space. There can be no doubt that in soil, this situation is the rule and the presence of Fe chelates formed by soil-born organic compounds in the bulk soil is the exception. So, it seemed worthwhile to concentrate our research on inorganic Fe and study the conditions under which different plant species can utilize this source of Fe for a normal growth.

In these studies, the root surface and the rhizosphere are of primary importance for the utilization of inorganic Fe, whereas with Fe chelates the diffusion of the chelate into the free space, its uptake into the root cell or its reduction prior to uptake at the plasmalemma, as assumed by Chaney *et al.* [9], might be of particular importance.

In order to have well-defined and controlled conditions with respect to ion concentration, pH and E_h in the root medium, most of our experiments were performed in water culture. Corn (*Zea mays*) and sunflower (*Helianthus annuus*) were used.

In a nutrient solution of the Hoagland type with NO_3^- as a source of N, due to preferential anion uptake compared to the cations, the pH increases during the growth. With corn plants [18, 21] there is no effect of the Fe supply on this pH increase. With FeEDTA (sufficient Fe nutrition), there is the same pH increase as with inorganic Fe-III (added as $Fe(OH)_3$) as without Fe at all (Fig. 2). In this well-aerated nutrient solution of pH 7.0, the availability of inorganic Fe-III to the plants is so low that these plants show the same severe chlorosis as without Fe supply, although the roots are covered with the $Fe(OH)_3$ precipitate. Considering the solubility product of inorganic Fe-III at this pH, this chlorosis is not surprising.
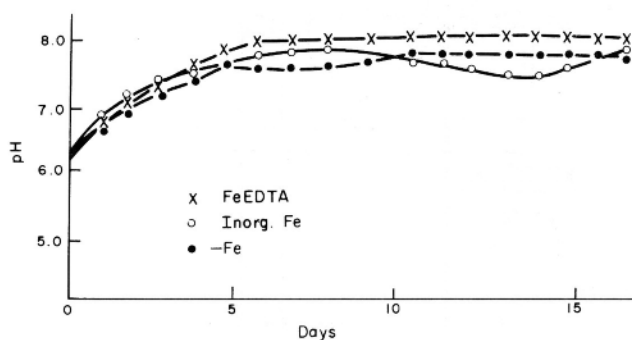

Fig. 2. Effect of different iron supply to corn plants on the pH changes in the nutrient solution. After Marschner *et al.* [21].

Artificially lowering the pH by adding acids to the nutrient solution increases the solubility of inorganic Fe-III and the availability of this source of Fe for corn plants [18]. Although, based on calculations of the solubility product of inorganic Fe in these well-aerated solutions, the concentration of ionic Fe is still very low even at pH 4 (in the range of 10^{-10} mole = below 10^{-8} mg Fe/litre), the plants grew well and were the normal green colour. As the plant roots were covered with the $Fe(OH)_3$ precipitates under these conditions it is likely, however, that this close contact between the Fe source and the root surface enabled the plants to mobilize more inorganic Fe than would be predicted from the solubility product in the nutrient solution.

The importance of the amount of $Fe(OH)_3$ precipitate at the root surface for mobilization and uptake of Fe by corn plants is further stressed by the next experiment where at a constant pH of 6.5, the amount of $Fe(OH)_3$ in the nutrient solution was increased from 10^{-5} M to 10^{-2} M (Table 7). Up to 10^{-3} M iron the growth rate and the chlorophyll and Fe contents were increased. At 10^{-2} M Fe supply, however, the growth rate drastically declined obviously as a result of the inhibition in P uptake, reflected in the very low P contents in the shoots. This demonstrates the strong interaction between Fe and P nutrition especially with supply of inorganic Fe.

Table 7.   Effect of increasing amounts of $Fe(OH)_3$ in the nutrient solution on growth and content of chlorophyll, Fe and P in corn plants*

Fe concn, M/l	DM		Content in the DM of the shoot		
	shoot (g)	root (g)	Chlorophyll (mg/g)	Fe (μg/g)	P (mg/g)
0	1.40	0.50	1.9	26.1	16.5
10^{-5}	1.75	0.66	3.4	26.8	14.0
10^{-4}	2.68	0.91	5.5	30.0	14.4
10^{-3}	5.33	1.20	12.1	71.7	3.8
10^{-2}	2.75	1.20	14.7	101.9	1.3

*After Azarabadi and Marschner [2]. P concentration 10^{-4} M/l.

This P–Fe interaction is well documented in the literature [6, 17] and special attention has been paid to the depressing effect of P on Fe uptake as one of the main problems in Fe nutrition of plants. Higher P concentrations in the substrate not only decrease the concentration of Fe^{3+} by precipitation of $Fe-III-PO_4$ but P also seems to shift the equilibrium between Fe-II and Fe-III towards Fe-III as demonstrated by Cher and Davison [10]. As Fe^{2+} is the main form of Fe available for the plants, the presence of P at the root surface or at the uptake sites of the root cells decreases the Fe availability for the plant.

This depressing effect of P on Fe nutrition of corn plants has been demonstrated with Fe chelates by Brown [6] and we could demonstrate this with inorganic Fe-III (Table 8).

At a constant pH of 6.5, increasing concentrations of P depress the growth of corn plants and increase the symptoms of Fe chlorosis. At very low concentrations of P (10^{-5} M), the plants obviously are able to utilize inorganic Fe-III at pH 6.5; however, this P concentration is so low that simultaneously severe symptoms of P deficiency occur and the P contents of the plants are in the range of strong deficiency. Contents of more than

1.5 mg P/g DM which reflect sufficient P supply, however, are combined with symptoms of Fe chlorosis.

Table 8.   Effect of increasing P concentrations in water culture on growth, chlorophyll and P content of corn plants*

M P / 1	g DM	mg/g Chlorophyll	P
10^{-5}	2.1	12.1	1.5
5×10^{-5}	2.6	5.1	1.7
10^{-4}	1.8	4.6	10.1
5×10^{-4}	1.1	2.8	10.7

*After Azarabadi and Marschner [2]. 5×10^{-4} M Fe/l as $Fe(OH)_3$.

The strong P–Fe interaction demonstrates the difficulty in having both proper Fe and P nutrition of corn at this pH of the nutrient solution and with inorganic Fe-III. Nevertheless, these experiments demonstrate that corn plants can utilize inorganic Fe-III even at a high pH and a high redox potential and that P is the determining factor in the utilization of inorganic Fe-III at high pH values.

The interference between Fe and P might occur in the substrate by precipitation or at the root surface by interference of P in the Fe reduction. There is, however, the possibility of a P–Fe interaction within the root and the translocation path to the shoot.

To elucidate this, Kashirad et al. [19] supplied P and inorganic Fe-III to different zones of the primary root of corn plants and demonstrated that the interactions between P and inorganic Fe within the plant root and shoot was small compared to the interactions in the substrate and at the root surface. This result has been further supported by experiments with the split-root technique [2].

The results of the P–Fe interaction seem to be in disagreement with field observations where even in soils well aerated and high in pH, corn plants seldom become chlorotic, although P and Fe are simultaneously present in the substrate. According to other results [2] on the "substrate effect" in Fe nutrition, in solid substrates like quartz sand or soil, the "exhaustion zone" of P around the root enables the plant roots to utilize inorganic Fe-III as source of Fe from this "exhaustion zone" even in presence of relatively high P concentrations in the bulk substrate. Besides other changes within the soil/root interface, the "exhaustion zone" of P seems to be one of the important factors responsible for the "rhizosphere effect" in utilization of inorganic Fe-III from solid substrates by plant roots.

The importance of this interface for utilization of inorganic Fe-III has been demonstrated by Jenny [14] using the dicotyledon species alfalfa. In dicotyledon species, however, the process of Fe mobilization at the root surface is much more complex. In contrast to monocotyledon species like corn, dicotyledon species like sunflower respond actively to Fe stress by changing the pH of the substrate and mobilization of inorganic Fe-III by reducing it to Fe-II even in a nutrient solution in the presence of P. This pH lowering is not caused by increased release of organic acids from the roots but by a shift in cation/anion uptake. Under Fe stress the cation uptake remains almost constant

whereas the anion uptake sharply decreases leading to excessive H^+ release (for charge compensation) and corresponding pH decrease [26, 27].

In the presence of inorganic Fe-III in the substrate, this lowering of the pH causes mobilization of Fe-III via reduction to Fe^{2+} and increased Fe uptake. The Fe stress is overcome rapidly and the cation/anion uptake is normalized, leading to an increase in pH. Considerable changes in the pH of the substrate can therefore occur with inorganic Fe-III as source of Fe as demonstrated in Fig. 3. This iron-stress response is an inherent property of the sunflower plant and microorganisms in the rhizosphere are not necessarily involved in this process [20].
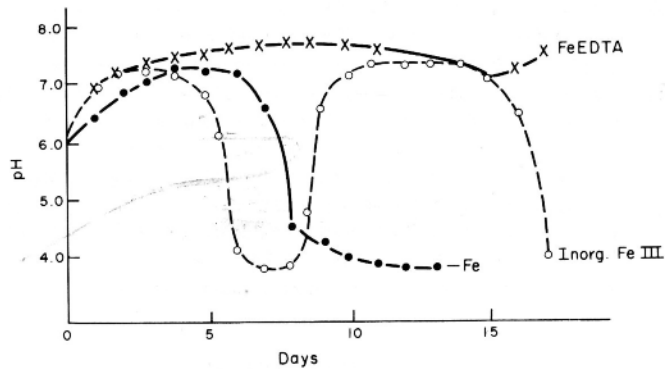
Fig. 3. Effect of different iron supplies to sunflower plants on the pH changes in the nutrient solution. After Marschner *et al.* [21].
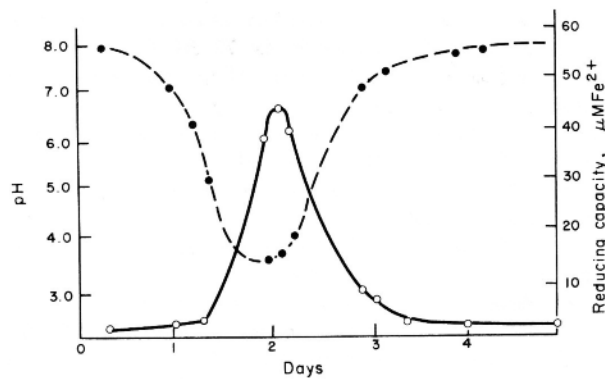
Fig. 4. Time course of pH value and reducing capacity of the nutrient solution with sunflower supplied with inorganic Fe-III. After Marschner *et al.* [21].

From this ability to mobilize inorganic Fe-III via a decrease in pH and release of reducing substances (Fig. 4) even in a nutrient solution other plant species can make a gain as shown in experiments with mixed culture of sunflower and corn [17].

The ability of plant species like sunflower, cotton or tomato to lower the pH even in a nutrient solution makes it understandable that in solid substrates like sand or soil under conditions of Fe stress, the pH in the rhizosphere of these plant species might rapidly drop within a short period of time and mobilize inorganic Fe-III by reduction processes. This leads to increased Fe uptake and normalization of the Fe nutrition with a corresponding increase in the pH of the rhizosphere. These pH fluctuations might take place quite often in the rhizosphere of soils with a high pH during the life cycle of a plant, perhaps only in certain root zones or portions of the root, though intensively enough to maintain a more or less constant Fe mobilization from the soil. These processes within the rhizosphere enable the roots of higher plants to create their own environment at least at the root/soil interface, an environment which is essential for a normal mineral nutrition of the plants under extreme conditions with respect to the soil pH.

The degree of the ability to change this root environment differs between plant species and ecotypes. A better understanding of the conditions within the rhizosphere and the mechanisms of regulation of this environment by the plant roots and by the microorganisms within the rhizosphere might enable us to support the plants in this respect or to select plant species and varieties better adapted to extreme ecological conditions or just with higher efficiency in uptake of plant nutrients.

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