Table 2. Effect of FYM and NPK on HCN and starch content of tubers.

	O/FYM	N	P	K	NP	NK	PK	NPK	S.E.
HCN (μg/g)									
Without FYM	103	175	98	68	158	105	75	98	±2.34
With FYM	113	180	120	85	173	135	85	120	±6.75
Starch content (%)									
Without FYM	25.7	24.0	25.8	26.4	24.3	26.3	27.7	25.1	±0.49
With FYM	25.1	25.0	25.4	26.7	24.7	27.7	27.9	25.4	±1.41

cated that N alone or FYM + N gave a bitter taste and a harder texture. On the other hand, K alone or P + K gave a nonbitter taste and a softer texture.

It may be concluded that though nitrogen significantly increased the tuber yield, it considerably affected cooking quality, particularly taste. However, the addition of P + K to N improved the quality.

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Mineral Nutrition of Cassava and Adaptation to Low Fertility Conditions

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In experiments using solution culture techniques, cassava was shown to be more tolerant than maize and soybean to low pH and high levels of aluminium and manganese. The requirements for potassium, nitrogen, and calcium for maximum growth are comparable to other crops. In the case of phosphorus, the needs are higher than other crops. Nevertheless the data show that cassava tolerates low calcium, nitrogen, and potassium in the root zone better than other crops. The plant has an ability to bulk roots at low phosphorus levels.

Cassava has earned a reputation for being well adapted to soils of low fertility. Thus, the ability of cassava to produce some yield, albeit low, in subsistence agriculture systems on soils of low fertility status has contributed greatly to its success over other staple food crops. Despite claims that cassava cultivars adapted to low soil fertility conditions show reduced ability to respond to fertilizer application, the results of

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many experiments show that cassava yields in low fertility areas can be raised substantially through improved crop nutrition. Jacoby (1965) reported strong differences among cultivars in responsiveness to fertilizer application, whereas Spain et al. (1974) found large differences in fresh root yields of cassava cultivars grown at four different lime rates.

The major soils used for cassava production in Latin America, Africa, and Southeast Asia are moderately to strongly acid oxisols and ultisols located in the tropics. In addition to their inherently low fertility, many of these soils exhibit limited production potential because of acid soil infertility. Problems of low pH, aluminium and manganese toxicities, molybdenum and calcium deficiencies, and low phosphorus and potassium availability have been reviewed recently (Kamprath and Foy 1971, Pearson 1975). Results from liming experiments have indicated that large genetic differences in acid soil tolerance exist among cassava cultivars (Spain et al. 1974).

Work conducted at the University of Queensland during the past 5 years has been particularly directed toward understanding the nature of the adaptation of cassava to low fertility situations. In addition, physiological differences between cultivars in nutrient response have been studied using stem tip cuttings raised using a mist propagation procedure. Substantial effort has also been directed toward recording and describing symptoms of nutritional disorders of cassava.

Methods

Most of this work was conducted in dilute continuously flowing solution cultures. Use of this technique allows plants to be grown under conditions in which the root environment is closely defined with respect to temperature, pH, and nutrient ion concentrations. In as much as the solution concentration does not decrease with time as a result of plant uptake the system is analogous to that of a well-buffered soil (Loneragan 1968). Using this technique, experiments have been conducted to compare the effects of a range of constant solution pH's and constant concentrations of Al, K, Ca, NO_3, NH_4, and P on the growth of cassava and other selected species. Interest has centered upon the nature of the response curves, both in terms of plant growth and nutrient absorption. Of particular significance, however, are the solution concentrations at which the growth of cassava and other species are restricted, with or without any symptom expression.

In current work, attempts are being made to test the conclusions from flowing culture experiments on cassava and other species using a highly buffered soil that has been adjusted to a wide range of equilibrium soil solution concentrations.

In an experiment on root bulking, plants were grown in large pots of nutrient solution (22 l) to which frequent small additions of phosphorus were made to ensure the plants either had a nonlimiting supply of the element throughout the experiment or were subject continuously to moderate or severe phosphorus stress. This technique referred to as "programmed nutrient addition" has been used successfully with other crops (Asher and Cowie 1970).

In still other experiments, conventional solution culture techniques employing small volumes (2.2 l) of relatively concentrated nutrient solution (e.g. Hoagland-Arnon solution) have been used in the study of nutrient deficiency and toxicity symptoms and in establishing critical tissue nutrient concentrations for the growth of cassava.

Results

Response to Solution pH

Effects of solution pH ranging from 3.3 to 8.5 on the relative whole plant yields of cassava (cv. Nina), maize, and tomato are shown in Fig. 1. This experiment was conducted in the flowing solution culture units with pH automatically controlled to within ±0.1 pH of the designated value and with the concentrations of all essential elements maintained at adequate levels. All species were grown for 4 weeks before harvest. The pH optimum of cassava is quite normal, at about 5.5. However, more significant is the higher relative yield of cassava at the lowest solution pH values.

These results suggest that cassava possesses a greater tolerance to high hydrogen ion concentration per se (low pH) than either tomato or maize.

Response to Solution Aluminium Concentrations

Cassava, maize, and soybean were grown in flowing solution culture at six aluminium concentrations ranging from 0 to 160 μM. The

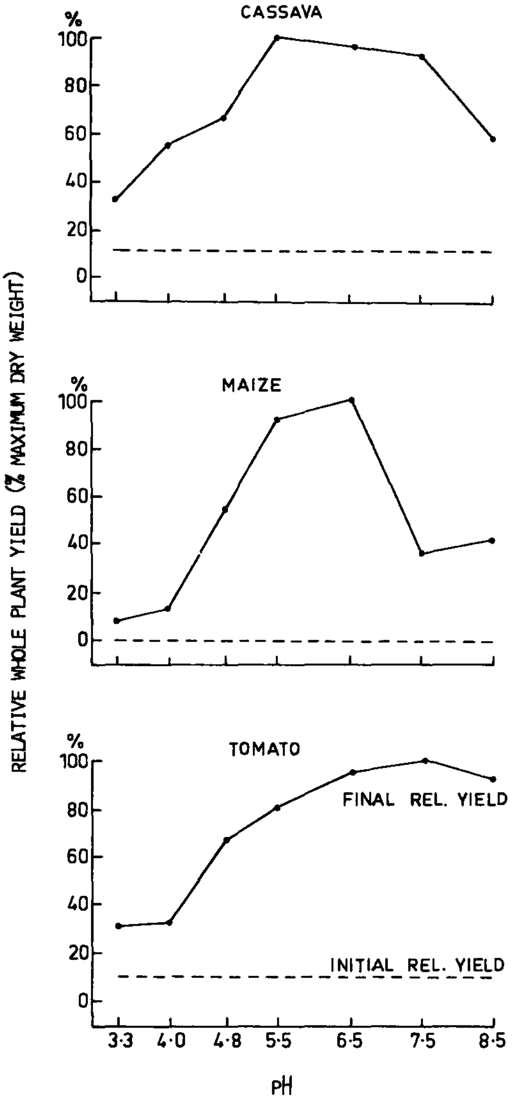

Fig. 1. Effect of nutrient solution pH on relative yield of cassava, maize, and tomato.

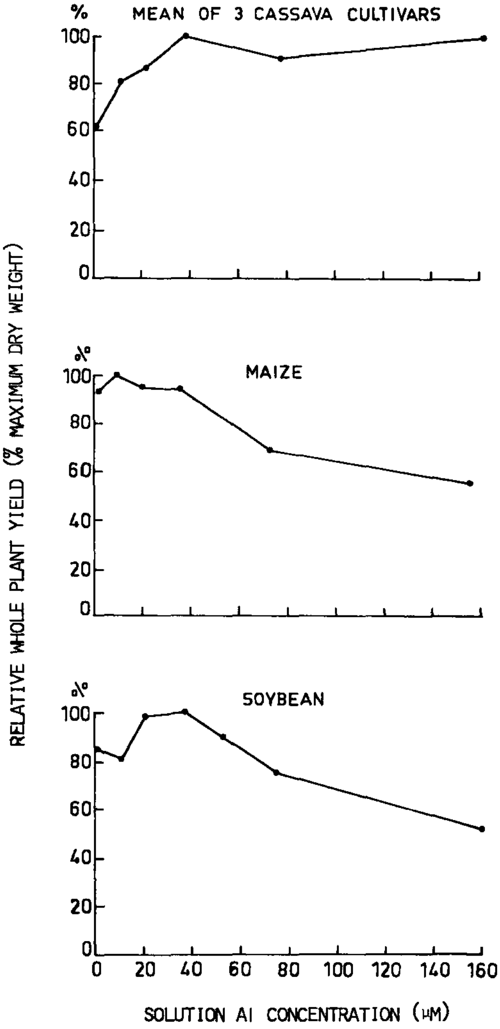

Fig. 2. Relative dry matter yield of whole plants as a function of concentrations of aluminium in solution.

solution pH was maintained at 4.2 ± 0.1 for the duration of the experiment. The response curves indicate that cassava is, on average, more tolerant to high solution aluminium concentrations than either maize or soybean (Fig. 2). At high solution aluminium, no obvious symptoms of root injury were exhibited by any of the cassava cultivars, whereas the roots of both maize and soybean showed severe injury symptoms, notably stunted and irregular lateral root development.

However, considerable variation in yield response to aluminium was found to exist among the three cassava cultivars studied. Cultivar CUQ2 achieved maximum yield at the highest aluminium concentration, while cultivar CUQ5 showed considerable sensitivity to the higher aluminium concentrations. All three cultivars showed a positive yield response to low concentrations of aluminium. The mechanism responsible for this effect is not known despite a previous report of this effect in pasture legumes tolerant to high solution aluminium concentrations (Andrew et al. 1973).

Table 1. External solution concentrations (μmol/litre) of potassium, calcium, nitrogen (ammonium and nitrate forms), and phosphorus required for maximal growth of cassava and four other crops.

	Element (or ion)				
	K	Ca	NH_4	NO_3	P
Cassava					
lowest conc.	8(9)[a]	101(2)[b]	7(1)	525(3)	50(6)
highest conc.	125(3)	—	489(5)	5100(8)	127(6)
Soybean	—	1035	—	—	0.7
Maize	8	3	7	52	3
Sorghum	—	10	489	525	—
Sunflower	32	101	29	525	—

[a] Figures in brackets indicate number of cultivars reaching maximal growth at the specified concentration.

[b] Both cultivars reached maximum yield at the same concentration.

The results obtained indicate that cassava cultivars show a range of adaptation to high solution aluminium concentrations, with one cultivar showing behaviour similar to the poorly tolerant maize and soybean, whereas the other two cultivars were much more highly tolerant.

Manganese Toxicity

No detailed studies of the tolerance of cassava cultivars to manganese toxicity have yet been made. However, a recent conventional solution culture experiment with a single cultivar CUQ2 suggests that very high external manganese concentrations (> 2000 μM) may be needed to cause recognizable symptoms and appreciable inhibition of growth. This growth inhibition was associated with a dramatic increase in manganese concentration in the plant and the development of a very pronounced interveinal chlorosis in the younger leaves. The failure of Howell (1974) to obtain symptoms of manganese toxicity other than temporary leaf wilting on hot days may have been due to an insufficient concentration of manganese (1000 μM) in the culture medium.

These results imply that cassava may be well adapted to those acid soils in which manganese toxicity limits the growth of other crop species. More detailed studies are required to confirm this suggestion.

Table 2. Relative yield of cassava and other crop species at the lowest constant solution concentrations (μM) used in various flowing culture experiments.

	Element (or ion)				
	K (0.5)	Ca (0.5)	NH_4 (0.4)	NO_3 (0.4)	P (0.05)
Cassava					
mean	52	26[a]	40	20	18
range	32–71	—	29–55	14–27	12–26
Soybean	—	2	—	—	34
Maize	36	2	7	6	21
Sorghum	—	3	5	2	—
Sunflower	43	0.2	9	3	—

[a] Relative yield the same for each of the two cultivars studied.

External Solution Concentrations for Maximal Growth

The external solution concentrations of potassium, calcium, nitrogen (ammonium and nitrate forms), and phosphorus required at the plant root surfaces for maximal growth of cassava and four other crop species are presented in Table 1. These data were obtained from a series of flowing solution culture experiments in which the solution pH was held constant (usually at 6.0 ± 0.1) throughout the duration of the experiment. The number of cassava cultivars used in the individual experiments ranged from 2 in the calcium experiment to 12 in the potassium and phosphorus experiments.

For potassium, calcium, and ammonium nitrogen, the external concentrations needed for maximal yields of the cassava cultivars are roughly comparable with those required for maximal yields of the other species studied. However, for nitrate nitrogen and in particular for phosphorus, in general higher external concentrations were needed to achieve maximal growth of cassava than for the other crop species. Thus, in the case of nitrate, eight of the eleven cultivars only reached maximal yield at the highest concentration studied (5100 μM), whereas none of the other crop species required more than 525 μM for maximal yield (Table 1). In the case of phosphorus, the contrast between cassava and the other crops was even greater. Indeed, the concentrations needed for maximal growth (50–127 μM) are higher than those of any other species reported in the literature (Asher and Loneragan 1967) with the possible exception of potato (Hougland 1947).

Table 3. Concentrations of individual elements in the plant tops at the lowest continuously maintained solution concentrations (μM). Plant concentrations are expressed on a g/100 g dry weight basis.

	Element (or ion)				
	K (0.5)	Ca (0.5)	$N(NH_4)$ (0.4)	$N(NO_3)$ (0.4)	P (0.05)
Cassava					
mean	0.68	0.23	1.30	1.38	0.08
range	0.58–0.82	0.10–0.35	n.a.	n.a.	0.06–0.11
Soybean	—	n.d.	—	—	0.13
Maize	0.89	0.23	0.70	1.20	0.10
Sorghum	—	0.11	1.10	1.10	—
Sunflower	1.04	n.d.	0.90	1.10	—

NOTE: n.a. — not available; n.d. — not determined, insufficient material.

The much higher solution requirements for phosphorus and nitrate exhibited by cassava suggest that, for maximum growth, cassava may require even higher levels of soil fertility than other common crop species.

Ability to Grow at Low External Nutrient Concentrations

The relative dry matter yields of cassava and four other crop species grown in flowing solution culture at the lowest solution concentrations tested for potassium, calcium, nitrogen (ammonium and nitrate), and phosphorus are presented in Table 2. For calcium and both forms of nitrogen, cassava was outstanding in its ability to grow under external nutrient concentration conditions that drastically limited the growth of the other species. For example, a solution calcium concentration of 0.5 μM reduced the yields of the other four crops to from 0.2 to 3% of maximum, whereas both cassava cultivars studied were able to achieve 26% of maximum yield in this treatment. In the case of potassium, where the deficiencies were not so severe in the other crops, cassava achieved a generally higher relative yield. However, cassava did not appear to possess any special advantage over the other species at the lowest phosphorus concentration.

These data provide clear evidence that cassava is able to tolerate low calcium, nitrogen, and potassium in the root environment better than the other species. This adaptation could well be of considerable significance in the success of cassava in low fertility field situations.

Tissue Concentrations at Lowest Solution Concentrations

The concentrations of potassium, calcium, nitrogen, and phosphorus in the plant tops at the lowest continuously maintained solution concentrations in the various individual flowing culture experiments are presented in Table 3. The mean concentrations of potassium and phosphorus were lower in cassava than in the other crop species, while the mean concentrations of nitrogen were higher than those in the other species. These concentration differences between cassava and the other species in themselves provide no evidence for adaptation to low fertility conditions. However, comparison of the plant tissue concentration data with the yield data (Table 2) does provide a means for assessing how efficiently the various nutrient elements are utilized in dry matter production by cassava and the other species. This comparison provides evidence for an adaptation of cassava to low fertility conditions with respect of both potassium and nitrogen, but not phosphorus. Thus, the association of lower potassium concentrations in the tops of cassava (Table 3) with higher relative yields (Table 2) suggests an adaptation in that cassava utilizes potassium more efficiently in dry matter production than the other species. The association of somewhat higher nitrogen concentrations in the tops of cassava than other species with the very much greater relative yields of cassava than other species also suggests a more efficient utilization of nitrogen in dry matter production by cassava. By contrast, the association of lower phosphorus concentrations in the

Table 4. Minimum nutrient concentrations in the tops of cassava and four other crop species at which plants were completely free of deficiency symptoms. Concentrations in g/100 g dry weight.

	K	Ca	P
Cassava			
mean	2.13	0.41	0.11
range	1.04–3.23	0.29–0.53	0.09–0.15
Soybean	—	2.70	0.22
Maize	4.30	0.20	0.42
Sorghum	—	0.38	—
Sunflower	6.91	1.97	—

tops of cassava with lower relative yields does not provide any evidence of adaptation. No trends are discernible in the case of calcium because of insufficient data.

Symptomless Growth Reduction

The minimum nutrient concentrations in the tops of cassava and other crop species at which plants were totally free of potassium, calcium, and phosphorus deficiency symptoms are shown in Table 4. Cassava was free of phosphorus and potassium deficiency symptoms at substantially lower plant tissue concentrations than other species. In the case of calcium, the concentrations necessary in cassava tops to prevent the development of symptoms were above those of the monocotyledons maize and sorghum, but well below those of the dicotyledons sunflower and soybean. In the case of phosphorus, all species were generally free of symptoms at the same solution concentration, viz. 0.7 μM phosphorus (Jintakanon, pers. comm.). At this concentration, the relative yield of cassava and also the phosphorus concentration in the tops of cassava were less than in soybean and maize. The apparent ability of cassava to regulate its growth under low solution phosphorus concentrations is believed to represent a further mechanism of adaptation to low soil fertility conditions.

The various studies have demonstrated that cassava tends to retain its older leaves on the plant to a much greater degree than other species when a nutrient stress is imposed. Spear et al. (1976) have observed much smaller differences in potassium concentration between the older leaves of cassava than other species when grown at adequate and limiting solution potassium concentrations.

In addition, Spear et al. (1976) observed comparatively little decline in potassium concentration with age in the leaves of cassava plants grown at the lowest solution potassium concentration (0.5 μM), whereas both maize and sunflower exhibited a strong gradient in declining leaf potassium concentration with increasing leaf age. Forno (pers. comm.) also observed that the oldest one or two leaves remained dark green compared with younger leaves when cassava was grown at very low external nitrogen concentrations (0.4 μM). These observations suggest that cassava possesses an abnormally low phloem mobility when compared with the other crop species. They also suggest an adaptation to low fertility conditions in that under sustained, but low nutrient supply cassava can adjust its rates of growth downward to match the low rates of nutrient uptake, thereby obviating the need for remobilization of nutrients from older leaves.

Effects of Phosphorus Stress on Root Bulking

All the experiments discussed so far have been of short-term duration and never more than 4 weeks. Accordingly, no consideration has been given to the production of the major harvestable part of the plant, viz. the large, swollen roots, under conditions where a particular nutrient stress is applied.

A longer term solution culture experiment using the programed nutrient approach (Asher and Cowie 1970) referred to earlier was conducted with the objective of determining the effect of a continuously maintained phosphorus stress on root bulking in cassava. Bulking was markedly reduced by phosphorus stress. However, stress effects on root bulking were much less than stress effects on the production of plant tops. At the final harvest on day 108, moderate and severe phosphorus stress resulted in relative top dry matter yields of 62 and 27% respectively, while the comparable relative yields of swollen roots were 76 and 44%, respectively. A comparison of the yield of thickened roots with top yields suggests that the severely stressed plants were considerably more efficient in that they produced a greater yield of swollen roots per unit weight of plant tops than the control plants, even though the absolute yield of roots was less. This compensation represents another adaptive mechanism that may explain some of the success of cassava in low fertility soils.

No phosphorus deficiency symptoms were observed on the severely stressed cassava plants until the closing stages of the experiment despite the 73% reduction in the yield of tops. In fact, in the absence of the nonstressed control and the moderately stressed plants, no basis would exist for believing that the growth of the severely stressed plants was anything other than normal. This ability to match growth rate to nutrient supply may well be important in the success of cassava in low fertility soils, but also makes it difficult, in the absence of phosphorus rate experiments, to establish just how deficient a crop really is under actual field conditions.

Conclusions

Several features that may be associated with the special adaptation of cassava to low fertility situations, including high soil acidity, have been identified. These include the ability to maintain relative yields under low nitrogen, potassium, and calcium, the more efficient utilization of potassium and nitrogen in dry matter production, and the ability to regulate its growth under low nutrient supply conditions. This latter feature is strengthened by the abnormally low phloem mobility of some elements that these studies suggest are characteristic of cassava. The ability to proceed with root bulking under quite severe phosphorus stress may be another important feature in the success of cassava as a crop plant in poor soils. Evidence is also presented that tolerance to low pH per se, to high aluminium concentrations, and possibly to high manganese are features of importance in the adaptation of at least some cultivars to highly acid soils. They suggest explanations for the large differences in acid soil tolerance among cassava cultivars reported by Spain et al. (1974).

Any advantages that cassava may possess by virtue of the vertical or horizontal distribution of roots in low fertility soils would not be revealed in solution culture studies such as those described here. Furthermore, any special mechanisms that cassava may possess for solubilizing soil constituents, e.g. through an alteration of rhizosphere pH or redox potential, through excretion of chelates, or through mycorrhizal associations, would not be of significance in the solution culture studies. These aspects also require investigation.

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