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COMPARISON OF THE NUTRIO-PHYSIOLOGICAL CHARACTERISTICS BETWEEN SWEET POTATO AND POTATO IN RELATION TO THE TOLERANCE TO LOW NUTRIENT AND LOW pH CONDITIONS*

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Contents

I. INTRODUCTION

Among marginal soils, acid soils which have a low nutrient supply power, cover a wide area of the world, especially in the tropics[16,23]. Increasing population, a high food demand, and a limitation of areas suitable for agriculture have caused farmers to move onto unfavorable marginal land. In 1985, IBSRAM as cited by Dowdle and Von Uexkull[4] reported that in Indonesia, a tropical country, more than 82 million ha or 43% of the land is dominated by those acid and low nutrient soils which are classified as Ultisols and Oxisols. At the same time, such a non tropic area as Japan also has relatively high proportion of Andosols or Volcanic ash soils that are characterized by low pH and low nutrients especially phosphorus.

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Sweet potato (*Ipomoea batatas* L.) and potato (*Solanum tuberosum*) are kinds of important root and tuber crops which are relatively tolerant to low pH and low nutrient conditions. Since the harvested organ of sweet potato is tuberous roots which is modified from the roots while that of potato is tuber which is modified from the stems, it is therefore considered that the nutrio-physiological characteristics of the two crops are different.

There is a big gap in the yields of these crops between developing and developed countries. For instance the average yields of sweet potato and potato in Indonesia, a developing country, were respectively 9 and 11.5 ton/ha or 2.5 and 2.8 times lower than the yields in Japan, a developed country[5]. Farmers in Japan apply a large amount of lime, nitrogen, phosphorus, and potassium to make these soils more productive. On the other hand, socio-economic reasons limit developing countries, and consequently only a small amount or no fertilizer and lime are applied to root and tuber crops. Accordingly, the yield is limited and low.

Soil management methods used to improve crop production with the application of "necessary" amounts of fertilizer, lime and other amendments, which are commonly used in the developed countries, is called high-input soil management technology. On the other hand, the application of limited amounts of these amendments is known as low-input soil management technology[15]. In the most developing countries, because of many limiting factors, the second approach is more favored as a good alternative to attain a reasonable, though not necessarily maximum yield. To maximize the efficiency of a purchased input, it is important to employ improved species or varieties that have a strong tolerance to adverse soil conditions.

The growth response of sweet potato and potato to low nitrogen and low potassium conditions have been reported by several authors[11,14,18,19,26,29,31]. However, these investigations concentrate mainly on making clear the effect of low nitrogen and low potassium stress conditions on the growth and yield, the deficiency symptoms of the two crops, and their tolerance to low nitrogen and low potassium conditions. Their mechanisms, though, have not been studied precisely.

Phosphorus deficiency is one of the most widespread nutritional problems in such soils as Ultisols and Oxisols. The tolerance of sweet potato and potato to low phosphorus soils has been reported separately. It has been reported that the tolerance of sweet potato to low phosphorus soils was stronger than that of Chinese cabbage and lettuce[8] while that of potato was stronger than that of sugar beet, tomato, and cabbage, but weaker than that of rice, maize, and azuki bean[21]. However, the mechanisms of tolerance to low phosphorus conditions were not explained deeply in the two crops.

High aluminum, low pH and low phosphorus are often limiting factors for crop growth in acid soils. The interrelationships between low pH, high aluminum and low phosphorus, and their effect on crop growth is somewhat complicated [20,25]. It has been reported that the tolerance of sweet potato to soil acidity is stronger than that of yams and taniers, but is weaker than that of cassava[1].

Several mechanisms that allow tolerance to aluminum in the tolerant cultivars of sweet potato and potato have been reported[7,13,17]. Furthermore, the mechanisms that lead to the inhibition of root growth by aluminum have been described by several authors[6,12,15,22,30].

The purpose of this study is (1) to compare the tolerance to low nutrient conditions such as low nitrogen, low phosphorus and low potassium, and to acid soils with low pH-high Al-low P conditions between sweet potato and potato, (2) to clarify the nutriophysiological mechanisms of the tolerance, and (3) to provide basic information for managing the low nutrient and acid soils and for breeding varieties that tolerate these soils in order to obtain a reasonable yield with low-input technology.

Emphasis has been given to sweet potato in this study, because information regarding sweet potato especially the nutrio-physiological aspects, is limited. At the same time, sweet potato is a more important crop in tropical countries than potato, since sweet potato can adapt widely to various climatic conditions at low or high altitudes, while potato does not adapt well to climate conditions with a high temperature.

II. TOLERANCE TO LOW NITROGEN AND LOW POTASSIUM SOILS AND THE MECHANISMS

Experiment 1. Effect of low nitrogen and low potassium treatments on growth and the absorption characteristics of nitrogen and potassium under water culture condition.

Materials and methods

Vine cuttings of sweet potato var. Beniazuma and seed tubers of potato var. Danshakuimo were planted in vermiculite beds for 14 and 21 days, respectively. Four uniform young seedlings of each crop were transplanted in a plastic container containing 300 l aerated nutrient solution. Low nitrogen treatment (0.3 ppm N as NH_4NO_3), low potassium treatment (0.3 ppm K as KCl and $K_2SO_4=1:1$) and control treatment were given. Composition of the culture solution in the control treatment were (ppm) : 30 N (NH_4NO_3), 1.0 P (NaH_2PO_4), 30 K (K_2SO_4 and KCl=1 : 1), 50 Ca ($CaCl_2$), 20 Mg ($MgSO_4$), 2.0 Fe ($FeSO_4$), 0.5 Mn ($MnSO_4$), 0.5 B (H_3BO_4), 0.2 Zn ($ZnSO_4$), 0.01 Cu ($CuSO_4$), and 0.005 Mo ($(NH_4)_6Mo_7O_{24}$). The pH of the solution was maintained at 5.3 by adding 0.1 NaOH using an automatic pH regulator.

All plants were harvested at 21 days after transplanting. After washing with deionized water, plant samples were separated into shoots and roots. The samples were oven dried at 80°C for 48 hours and dry weights were determined. A part of root samples was determined for root length with an image processor[33].

Table 1. Dry weight of sweet potato and potato grown under the low N, the low K, and the control treatments at 21 days after transplanting (g/pℓ).

Treatment	Leaves	Petioles	Stems	Roots	Total
SWEET POTATO					
Low N	2.50	0.52	1.30	2.80	7.10
Low K	4.70	0.96	1.30	0.96	7.90
Control	10.20	2.90	4.20	3.40	20.60
POTATO					
Low N	0.21	0.04	0.41	0.15	0.81
Low K	0.64	0.10	0.50	0.19	1.40
Control	1.80	0.39	1.10	0.98	4.30

Table 2. Length, surface area, and mean diameter of roots of sweet and potato grown in the low N, the low K, and the control treatments at 21 days after transplanting.

Treatment	Root length		Surface area		Mean diameter	
	(m/pl)	(%)	(m^2/pl)	(%)	(mm)	(%)
SWEET POTATO						
Low N	105	36	0.25	42	0.74	119
Low K	66	22	0.15	25	0.58	94
Control	294	100	0.60	100	0.62	100
POTATO						
Low N	12	11	0.02	9	0.54	87
Low K	13	12	0.02	11	0.59	95
Control	109	100	0.21	100	0.62	100

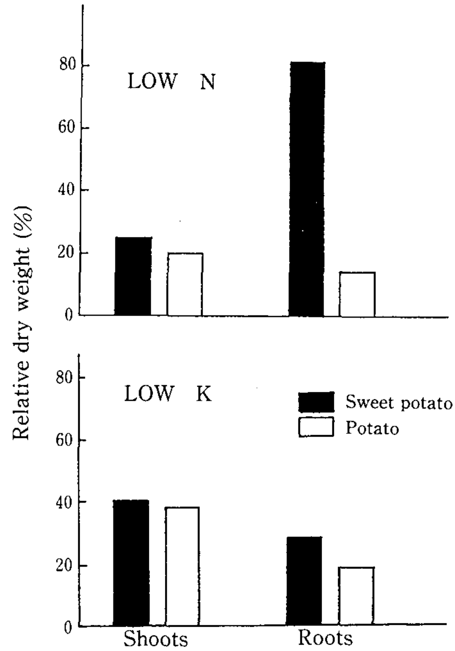

Fig. 1. Relative dry weight of shoots and roots of sweet potato and potato in the low N and low K treatments at 21 days after transplanting under water culture condition (Control = 100%).

Table 3. Nitrogen and potassium content of sweet potato and potato plants grown in the low nitrogen, the low potassium, and the control treatments at 21 days after transplanting.

Treatment	Leaves		Petioles		Stems		Roots	
	N%	K%	N%	K%	N%	K%	N%	K%
SWEET POTATO								
Low N	1.34	—	0.83	—	0.65	—	0.96	—
Low K	—	0.95	—	1.19	—	1.11	—	0.69
Control	2.65	3.65	3.30	7.19	3.58	3.46	3.84	4.69
POTATO								
Low N	2.47	—	1.78	—	1.07	—	2.29	—
Low K	—	0.74	—	1.13	—	1.11	—	0.71
Control	5.58	3.73	3.07	7.47	2.87	5.58	4.47	2.93

Table 4. Amount of nitrogen and potassium absorbed by sweet potato and potato grown in the low nitrogen, the low potassium, and the control treatments at 21 days after transplanting (mg/pl).

Treatment	Shoots				Roots				Total			
	N	(%)	K	(%)	N	(%)	K	(%)	N	(%)	K	(%)
SWEET POTATO												
Low N	46	9	—	—	27	21	—	—	73	11	—	—
Low K	—	—	71	10	—	—	7	4	—	—	77	9
Control	516	100	726	100	131	100	159	100	647	100	886	100
POTATO												
Low N	10	7	—	—	3	8	—	—	14	7	—	—
Low K	—	—	11	7	—	—	1	4	—	—	13	7
Control	144	100	158	100	44	100	29	100	188	100	186	100

Total nitrogen content of the plants were determined by micro-Kjeldahl meehod, and potassium content with a flame photometer.

Results

Dry matter productions of sweet potato and potato were significantly affected by the low N and the low K treatments under water culture condition (Table 1). Relative total dry weight of sweet potato and potato at 21 days after transplanting compared with the control treatment decreased considerably by the low nitrogen treatment of 0.3 ppm N (Fig. 1). Also in this treatment, that of sweet potato shoots was slightly higher than that of potato. On the other hand, that of sweet potato roots was 82% of the control treatment at 30 ppm N and was five times higher than that of potato roots.

In the low potassium treatment with 0.3 ppm K relative shoot dry weight of sweet potato and potato decreased in the similar degree, but it was better than that in the low nitrogen treatment (Fig. 1). Relative dry weight of roots was lower than that of shoots and was higher in sweet potato than in potato. The capability of sweet potato roots to grow and to elongate in the low nitrogen treatment was greater than that in the low potassium (Table 2).

Nitrogen content in the leaves, stems, petioles, and roots of sweet potato under the low nitrogen treatment was lower than that of potato (Table 3). However, in the low potassium treatment, potassium content in the plant tissues was similar in both crops.

The amounts of nitrogen and potassium absorbed by sweet potato were higher than those of potato (Table 4). Under the low nitrogen and the low potassium treatments, relative amounts of nitrogen and potassium absorbed by sweet potato compared with the control treatment were higher than those of potato.

Nitrogen and potassium use efficiencies which are expressed by the amount of total plant dry matter produced by a unit amount of nitrogen or potassium absorbed by plants are presented in Table 5. Nitrogen use efficiency of sweet potato was higher than that of potato in both the low nitrogen and control treatments. On the other hand, potassium use efficiency was similar between the two crops under both conditions.

Table 5. Nitrogen and potassium use efficiencies* of sweet potato and potato grown in the low N, the low K, and the control treatments at 21 days after transplanting.

Treatment	N use efficiency (gDW/gN)	N use efficiency (%)	K use efficiency (gDW/gK)	K use efficiency (%)
SWEET POTATO				
Low N	97.1	305	—	—
Low K	—	—	102.4	443
Control	31.8	100	23.1	100
POTATO				
Low N	59.0	258	—	—
Low K	—	—	109.6	474
Control	22.9	100	23.1	100

* Total amount of plant dry matter produced by a unit amount of nitrogen or potassium absorbed by plant

Experiment 2. Effect of low nitrogen and low potassium treatments under field condition.

Materials and methods

Even though the vine cuttings of sweet potato were transplanted in the field condition and the harvested organ of sweet potato was tuberous roots, the term "planting" and "tuber" instead of respective "transplanting" and "tuberous root" will be used in this paper in order to make the explanations simpler.

The same varieties of sweet potato and potato as described in Experiment 1 were planted in the experimental field of Hokkaido University in 1987.

Three treatments of $-N$ (N-P_2O_5-K_2O=0-100-100 kg/ha), $-K$ (100-100-0), and control (100-100-100) were applied to those crops. Nitrogen, phosphorus, and potassium sources used were ammonium sulfate, superphosphate, and potassium sulfate, respectively. The fertilizers were applied as a basal dressing shortly before planting. In the $-N$ plot, only phosphorus and potassium had been supplied for seventy years, while in the in the $-K$ plot, only phosphorus and nitrogen had been applied. Plot size was 10.6×5.3 m. Plant densities of sweet potato and potato were 40,000 and 55,556 plants/ha, respectively. In the early stage, sweet potato was protected by transparent vinyl cover put over young plants.

Chemico-physical properties of soils were determined from top soil of each plot which was collected just before planting. Plant samples were randomly collected three times, at the early growth stage, at the middle growth stage and at harvest. Plant samples were separated into leaves, petioles, stems, and tubers, except at the early growth stage where stems and petioles were not separated. The samples were then dried, weighed and analyzed as described in Experiment 1. Analysis of starch and sugar of the tubers was conducted by the Anthron method.

Results

Total nitrogen content of the soils in the $-N$ and the control treatments was

Table 6. Physico-chemical properties of soils in the-N, the-K, and the control treatments before planting in 1987

Soil properties	Treatment		
	$-N$	$-K$	Control
$pH(H_2O)$ (1:2.5)	5.7	5.4	5.2
Total N (%)	0.25	0.32	0.30
Exch. K (me/100g)*	1.1	0.22	0.63
Sand (%)	—	—	26.7
Silt (%)	—	—	30.7
Clay (%)	—	—	42.6

* 1 N NH_4-acetate at pH 7.0

Table 7. Dry weight and LAI of sweet potato and potato in the −N, the −K and the control treatments during growth in 1987 (kg/ha).

	−N			−K			Control		
	EGS*	MGS*	H*	EGS	MGS	H	EGS	MGS	H
SWEET POTATO									
Leaves	218	917	981	158	1221	1185	210	2026	1856
Stems**	118	828	1039	84	1220	1365	125	2798	2844
Shoots	336	1745	2020	242	2441	2550	335	4824	4700
Tubers	193	3758	5810	52	2879	3734	185	6511	9004
Total	529	5503	7830	294	5320	6284	520	11335	13704
LAI**	0.38	2.06	1.36	—	—	—	0.31	6.05	4.07
POTATO									
Leaves	144	453	—	360	865	—	674	827	—
Stems**	103	397	—	169	372	—	375	835	—
Shoots	247	850	463	529	1237	424	1049	1662	929
Tubers	191	2708	3597	315	3122	3714	677	8761	10687
Total	438	3558	4060	844	4359	4138	1726	10423	11616
LAI	0.15	1.24	—	—	—	—	0.85	2.87	—

* EGS = The early growth stage, MGS = The middle growth stage, H = Harvest
** Including petioles
*** Leaf area index (m^2/m^2)

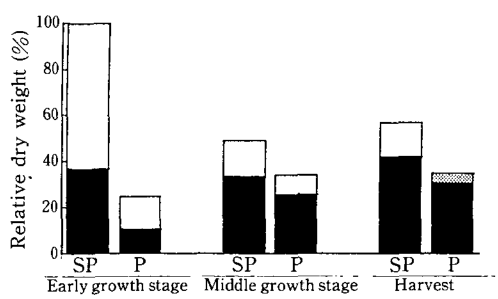

Fig. 2. Relative total dry weight of sweet potato (SP) and potato (P) under the −N treatment during growth (Control = 100%). Shoots ▭ Tubers ■, Dead shoots ▒

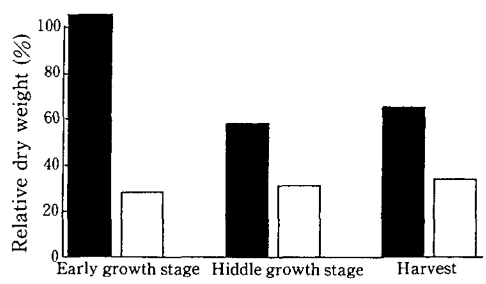

Fig. 3. Relative tuber dry weight of sweet potato ■ and potato ▭ under the −N treatment during growth (Control = 100%).

0.25 and 0.3%, respectively, while those of exchangeable potassium of the −K and the control treatments were 0.22 and 0.63 me/100 g, respectively (Table 6).

The tuber dry weights of sweet potato and potato in the control treatment were 9.0 and 10.7 ton/ha, respectively (Table 7). Although mean air temperature in Sapporo was 16.9°C in June and 21.0°C in August, 1987, sweet potato variety Beniazuma was able to produce tuber yield almost the same as that of potato.

Relative total dry weight of sweet potato in this condition was higher than that of potato throughout the growth (Figs 2 and 3). At the early growth stage, relative dry weight of sweet potato in the −N treatment was extremely high and was similar to the control treatment both in shoots and tubers. However, it was remarkably decreased at the later stages. At the middle growth stage, nitrogen

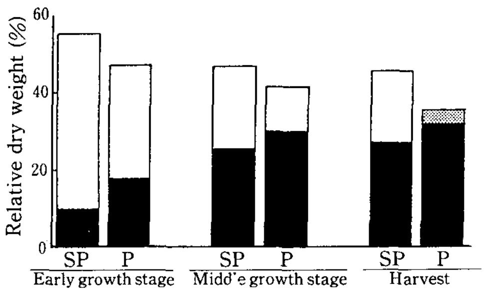

Fig. 4. Relative total dry weight of sweet potato (SP) and potato (P) under the −K treatment during growth (Control=100%). Shoots □ Tubers ■ Dead shoots ▒

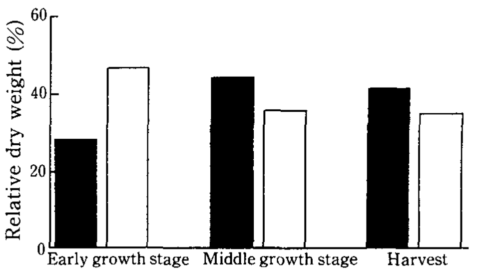

Fig. 5. Relative tuber dry weight of sweet potato ■ and potato □ under the −K treatment during growth (Control=100%).

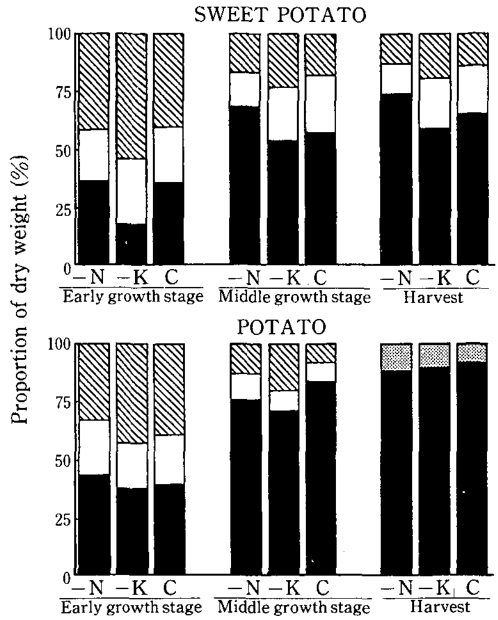

Fig. 6. Proportion of dryweight in the leaves ▧, stems □, tubers ■, and dead shoots ▒ of sweet potato and potato under the −N, the −K, and the control treatments during growth.

deficiency symptom appeared in the leaves, which was characterized by the appearance of strong purple color. On the other hand, growth of potato was poor from the early stage under the −N treatment. Nitrogen deficiency symptom had appeared in potato from the early stage.

Relative total dry weight and relative tuber yield of sweet potato in the −N treatment at the early growth stage were considerably greater than that of potato, however, the difference became smaller in the later stages (Figs. 2 and 3).

Relative total dry weights of both crops were remarkably decreased in the low potassium treatment (Fig. 4). However, that of sweet potato was slightly greater than that of potato. The relative tuber dry weight of sweet potato was lower at the early growth stage, but it became higher than that of potato at the middle growth stage and at harvest (Fig. 5).

Proportions of dry matter in the leaves, stems and tubers under the −N, the −K and the control treatments were different in both crops (Fig. 6). The proportions of tubers in all treatments increased with the growth while those of shoots decreased. In sweet potato, the proportion of tubers was higher than that in the control treatment but that of shoots was lower in the −N treatment. On the other hand, in the −K treatment, the proportion of tubers was lower than that

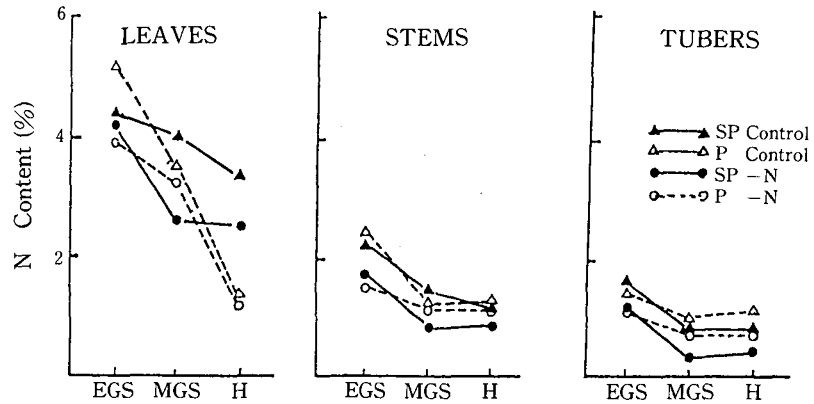

Fig. 7. Nitrogen content in the leaves, stems and tubers of sweet potato (SP) and potato (P) under the −N and the control treatments at the early growth stage (EGS), the middle growth stage (MGS) and at harvest (H) in 1987.

in the control treatment but that of shoots was higher. In potato, the proportion of tubers in the −N treatment was not significantly different from that in the control treatments. On the other hand, that in the −K treatment at the middle growth stage was considerably lower than that in the control while it is similar at the early growth stage and at harvest.

Nitrogen content in the leaves of both crops were relatively high at early growth stage and decreased in the later stages (Fig. 7). Eventually, N content of potato was considerably lower than that of sweet potato especially at harvest. On the other hand, in the −N treatment, nitrogen content in the leaves was similar in both crops, but that of potato was considerably lower in the later stages. During maturity, self-destruction of shoot occurred in potato and leaves were completely dead at harvest. At the early growth stage, nitrogen content in the leaves of sweet potato under the −N treatment was relatively high and similar with that in the control treatment. But at the middle growth stage it was greatly decreased in the −N treatment and was considerably lower than the

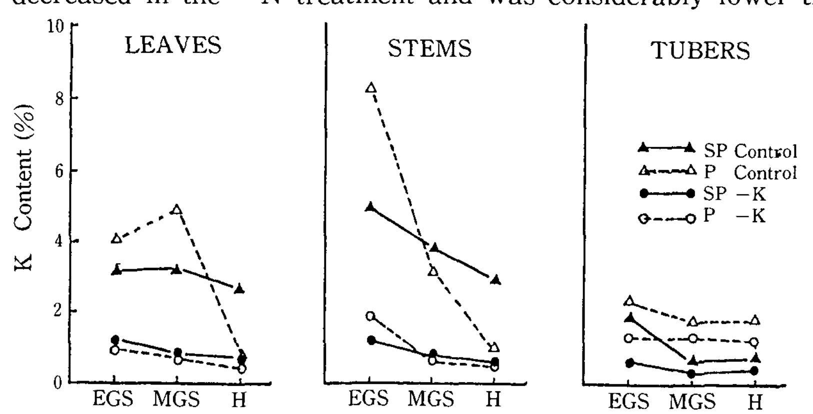

Fig. 8. Potassium content in the leaves, stems and tubers of sweet potato (SP) and potato (P) under the −K and the control treatments at the early growth stage (EGS), the middle growth stage (MGS), and at harvest (H) in 1987.

control. On the contrary, that of potato at the early growth stage was remarkably lower in the −N treatment compared to that of the control treatment. However, that of the control treatment decreased tremendously at the middle growth stage and it was similar in both treatments at harvest.

Nitrogen content in the stems and tubers of potato was higher than that of sweet potato especially at harvest, which was opposite to the nitrogen status in the leaves.

Potassium content in all plant tissues of potato at the early growth stage in the control treatment was higher than that of sweet potato (Fig. 8). Potassium content in the leaves of potato in the control treatment at the early and middle growth stages was higher than those of sweet potato, but the self-destruction of potato shoots during maturity reduced it strongly in the leaves at harvest and it became lower than that of sweet potato. Under the −K condition, that in the leaves of sweet potato was slightly higher than that of potato during growth. That in the stems of potato under the control treatment decreased strongly at the middle growth stage and it was continuously decreased until harvest. After the middle growth stage that in potato was lower than in sweet potato. On the other hand, those of sweet potato and potato in the −K treatment were similar. That in tubers of sweet potato was lower than that of potato in both the treatments and at all stages.

Amount of nitrogen absorbed by sweet potato at harvest was larger than that of potato both in the −N and the control treatments (Table 8). Relative amount

Table 8. Amount of nitrogen absorbed by sweet potato and potato in the −N and the control treatments during growth in 1987 (kg/ha)

	−N			Control		
	EGS*	MGS*	H*	EGS	MGS	H
SWEET POTATO						
Leaves	9.2	23.8	24.5	9.2	81.0	61.2
Stems**	2.0	6.8	8.9	2.8	38.9	31.9
Shoots	11.2	30.6	33.5	12.0	119.9	93.1
Tubers	2.3	12.0	22.7	3.0	51.4	71.1
Total	13.5	42.7	56.1	15.0	171.4	164.2
Rel. amount of N absorbed	90	25	34	100	100	100
POTATO						
Leaves	5.6	14.5	—	35.0	28.9	—
Stems**	1.5	4.4	—	9.0	10.0	—
Shoots	7.2	18.9	5.1	44.0	39.0	11.1
Tubers	2.1	19.0	25.2	9.5	85.9	117.6
Total	9.3	37.8	30.3	53.5	124.8	128.7
Rel. amount of N absorbed	17	30	24	100	100	100

* EGS = Early growth stage, MGS = Middle growth stage, and H = Harvest
** Including petioles

Table 9. Amount of potassium absorbed by sweet potato and potato in the −K and the control treatments during growth in 1987 (kg/ha).

	−K			Control		
	EGS*	MGS*	H*	EGS	MGS	H
SWEET POTATO						
Leaves	1.9	9.8	8.3	6.5	64.8	48.3
Stems**	1.0	8.1	8.1	6.1	104.6	80.5
Shoots	2.9	17.8	16.3	12.6	169.5	128.7
Tubers	0.4	9.5	15.3	3.5	42.3	63.9
Total	3.3	27.3	31.7	16.2	211.8	192.7
Rel. amount of K absorbed	20	13	16	100	100	100
POTATO						
Leaves	3.6	6.1	—	27.0	40.5	—
Stems**	3.2	2.1	—	31.5	26.7	—
Shoots	6.8	8.1	1.7	58.5	67.2	7.4
Tubers	4.1	39.6	44.6	15.6	156.8	192.4
Total	10.9	47.8	46.3	74.0	224.1	199.8
Rel. amount of K absorbed	15	21	23	100	100	100

* EGS = Early growth stage, MGS = Middle growth stage, and H = Harvest
** Including petioles

Table 10. Nitrogen and potassium efficiencies* of sweet potato and potato in the −N, the −K and the control treatments in 1987

Treatment	N efficiency		K efficiency	
	(gDW/gN)	(%)	(gDW/gK)	(%)
SWEET POTATO				
−N	104	189	—	—
−K	—	—	118	251
Control	55	100	47	100
POTATO				
−N	116	143	—	—
−K	—	—	80	151
Control	83	100	53	100

* Total amount of harvested organ produced by a unit amount of nitrogen or potassium absorbed by plant

Table 11. Moisture, sugar, starch and protein content (%) in the tuber of sweet potato and potato in the −N, the −K, and the control treatments in 1987.

	Moisture	Sugar	Starch	Protein
SWEET POTATO				
−N	70.0	11.6	50	2.4
−K	69.1	9.4	85	7.0
Control	69.1	10.7	77	4.9
POTATO				
−N	77.9	1.3	80	4.4
−K	77.2	1.6	80	10.0
Control	76.6	1.4	77	7.1

of nitrogen absorbed by sweet potato in the −N treatment compared with the control treatment was high in the early growth stage (90%) and markedly decreased at the later stages (25-34%). On the other hand, those of potato was lower throughout the growth (17-30%).

In the −K and the control treatments, total amount of potassium absorbed by both the crops increased tremendously at the middle growth stage and it was not changed thereafter (Table 9). The decrease of the total amount of potassium in the plant might be due to the falls of some old leaves and leaching from the plants.

Nitrogen and potassium efficiencies which are expressed by the amount of harvested organ produced by a unit amount of nitrogen or potassium absorbed by plant are presented in Table 10. Nitrogen efficiency of sweet potato in the −N treatment was lower than that of potato. However, the relative value of nitrogen efficiency of sweet potato in the −N treatment was 189% compared to the control and it was higher than that of potato (143%).

Potassium efficiency and relative value of potassium efficiency of sweet potato in the −K treatment were higher than those of potato.

Chemical composition of tubers was influenced by the −N and the −K treatments (Table 11). Crude protein of both crops and starch content of sweet potato were markedly decreased by the −N treatment. On the other hand, the crude protein under the −K treatment increased in both crops. Sugar content of sweet potato was higher in the −N treatment than that of the control treatment, while that in potato was similar in both treatments.

Experiment 3. Effect of nitrogen application levels on growth and nitrogen status under field condition.

Materials and methods

In 1989, sweet potato and potato were planted with the same method as described in Experiment 2. In this experiment, sweet potato and potato were planted with the same density (55,556 plants/ha) but no transparent vinyl cover was given to sweet potato.

Three levels of nitrogen application : 0 kg N/ha (N_0 treatment), 50 kg N/ha (N_1 treatment) and 100 kg N/ha (N_2 treatment) were applied to those crops.

Except at the N_0 treatment, plant samples were collected twice during growth, that is at the middle growth stage and at harvest. In the N_0 treatment, samples were taken nine times for sweet potato and seven times for potato at 2 weeks intervals.

Growth analysis following the WATSON method (1952) such as crop growth rate (CGR), net assimilation rate (NAR), and leaf area index (LAI) were calculated based on the data of dry weight and leaf area measured at each sampling time. The determination of plant dry weight and analysis of total nitrogen content in the plant were conducted by the same procedures as in Experiment 2.

Results

Dry matter production of the two crops in different levels of nitrogen application are shown in Table 12. At both of the middle growth stage and harvest, the relative total and tuber dry weights of sweet potato at N_0 and N_1 treatments compared to N_2 treatment were larger than those of potato (Figs. 9 and 10).

Table 12. Dry weight of sweet potato and potato in the different levels of nitrogen application at the middle growth stage (MGS) and at harvest (H) in 1989 (kg/ha).

	N_0		N_1		N_2	
	MGS	H	MGS	H	MGS	H
SWEET POTATO						
Leaves	482	714	1029	1450	1234	1550
Stems*	333	985	935	1640	1102	2040
Shoots	815	1699	1964	3090	2336	3590
Tubers	1500	4460	1858	6330	2391	6920
Total	2315	6159	3822	9420	4727	10510
POTATO						
Leaves	199	–	345	–	682	–
Stems*	94	–	201	–	337	–
Shoots	293	160	546	290	1019	569
Tubers	1343	2107	2751	4640	4616	5488
Total	1636	2267	3297	4930	5635	6057

* Including petioles

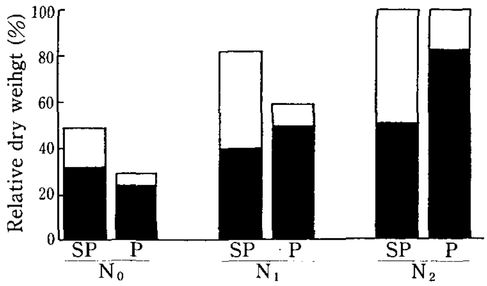

Fig. 9. Effect of nitrogen appication rates on relative total dry weight of sweet potato (SP) and potato (P) at the middle growth stage. Shoots □ Tubers ■

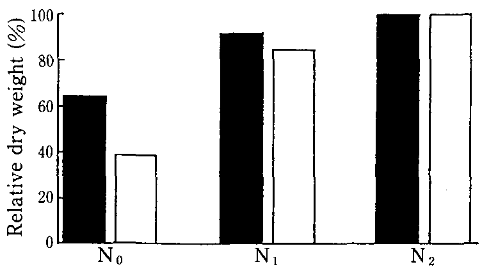

Fig. 10. Effect of nitrogen application rates on relative tuber dry weight of sweet potato ■ and potato □ at harvest.

Nitrogen content in the tubers of sweet potato was lower than those of potato in all treatments both at the middle growth stage and at harvest (Table 13). The difference in nitrogen content between tubers of both crops was larger at N_0 treatment but gradually decreased at N_1 and N_2 treatments. That in the leaves of sweet potato at the middle growth stage was lower at N_0 treatment than that of potato, but it was higher at N_1 and at N_2 treatments than that of potato.

Nitrogen application increased the amount of nitrogen absorbed by both crops (Table 14). The amount of nitrogen absorbed by sweet potato was higher than that of potato in all stages at all nitrogen application treatments.

The nitrogen efficiency at N_0 treatment was the same in both crops (Table 15). On the other hand, under the high nitrogen application treatments, those of sweet potato were lower than those of potato. The percentage of amount of nitrogen absorbed to the amount of nitrogen fertilizer applied was also decreased in the high nitrogen rates (N_2 treatment), and that of sweet potato was higher than that of potato.

Changing pattern of dry weight during growth of sweet potato and potato at N_0 treatment was different (Fig. 11). Dry matter production of potato was larger at the early stage and the total and the tuber dry weight reached maximum around 9 weeks after emergence, and then was kept almost constant until harvest.

Table 13. Nitrogen content (%) in the leaves, stems and tubers of sweet potato and potato in the different levels of nitrogen application at the middle growth stage (MGS) and at harvest (H) in 1989.

	N_0		N_1		N_2	
	MGS*	H*	MGS	H	MGS	H
SWEET POTATO						
Leaves	3.13	3.00	4.97	3.80	4.90	4.00
Stems*	1.01	1.07	1.37	1.27	1.69	1.57
Tubers	0.39	0.39	0.82	0.59	1.10	0.78
POTATO						
Leaves	4.11	—	4.02	—	4.39	—
Stems*	1.45	—	1.45	—	1.55	—
Dead shoots	—	1.37	—	1.40	—	1.50
Tubers	0.87	1.01	1.11	1.14	1.22	1.20

* Including petioles

Table 14. Amount of nitrogen absorbed by sweet potato and potato in the different levels of nitrogen application at the middle growth stage (MGS) and at harvest (H) in 1989 (kg/ha).

Treatment	Dosage (kg/ha)	SWEET POTATO				POTATO			
		MGS*	(%)	H*	(%)	MGS	(%)	H	(%)
N_0	0	24	23	49	33	21	23	23	31
N_1	50	79	75	113	76	47	52	57	77
N_2	100	105	100	148	100	91	100	74	100

Table 15. Nitrogen efficiency and percentage of amount of nitrogen absorbed by sweet potato and potato at different levels of nitrogen application.

Treatment	Dosage (kg N/ha)	SWEET POTATO		POTATO	
		N efficiency* (g dw/g N)	Absorption percentage** (%)	N efficiency (g dw/g N)	Absorption percentage (%)
N_0	0	90	—	90	—
N_1	50	56	128	81	67
N_2	100	47	99	74	51

* Amount of harvested organ produced by a unit amount of nitrogen absorbed by crops
** Percentage of amount of nitrogen absorbed by crop to amount of nitrogen fertilizer applied.

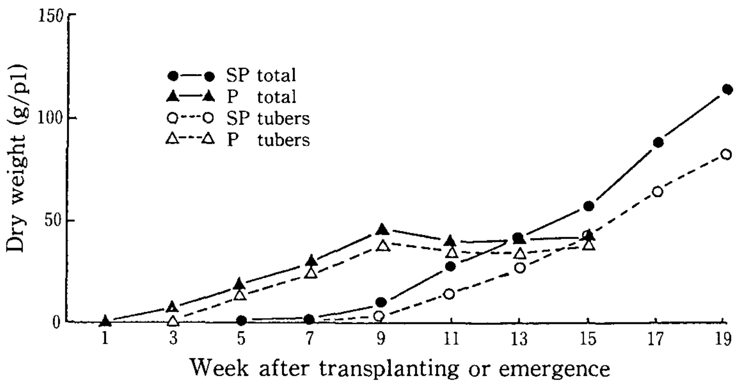

Fig. 11. Changes of dry weight with time after transplanting in sweet potato (SP) and after emergence in potato (P) under the N_0 treatment during growth.

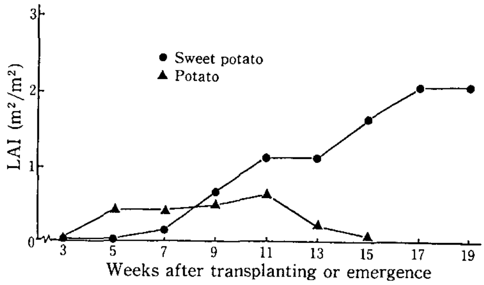

Fig. 12. Leaf area index (LAI) of sweet potato and potato under the N_0 treatment during growth.

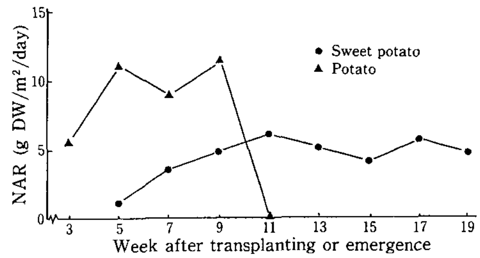

Fig. 13. Net assimilation rate (NAR) of sweet potato and potato under the N_0 treatment during growth.

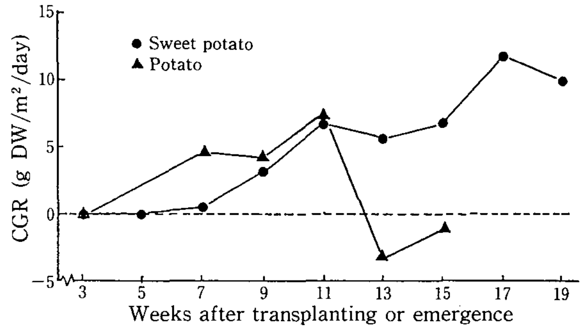

Fig. 14. Crop growth rate (CGR) of sweet potato and potato under the N_0 treatment during growth.

On the other hand, dry weight of sweet potato increased slowly at early stage and then increased rapidly after 9 weeks until harvest. Total dry weight of sweet potato became larger than potato after 13 weeks and that of tubers became larger after 15 weeks after transplanting.

Leaf area index (LAI) of sweet potato gradually increased until 17 weeks after transplanting and became constant (Fig. 12). The maximum LAI of sweet potato was 2.04 at N_0 treatment. LAI of potato increased rapidly at early stage, increased gradually after 5 weeks and reached maximum (0.63) and then markedly decreased after 11 weeks.

Net assimilation rate (NAR) of sweet potato was lower than that of potato from the early growth stage to 10 weeks after transplanting (Fig. 13). Since that of potato was strongly decreased at the later stage, that of sweet potato became larger thereafter. The maximum NAR of potato was 11.4 g DW/m^2/day, and it was almost two times higher than that of sweet potato.

Crop growth rate (CGR) of both crops were shown in Fig. 14. The CGR of sweet potato was smaller in the early growth stage than that of potato. But it was gradually increased until harvest. On the other hand, that of potato decreased tremendously at the later stage. As a result, CGR became higher in sweet potato about 11 weeks after transplanting than in potato.

Experiment 4. ^{15}N distribution pattern in the plant under the low nitrogen and the control treatments.

Materials and methods

The uniform young seedlings were transplanted in plastic pots containing 10 liter vermiculite. Five hundred ml of the nutrient solution was applied to each pot from the bottom hole at two days interval. Composition of nutrient solution except nitrogen was the same as in Experiment 1.

After growing under 15 ppm ^{14}N as NH_4NO_3 for 25 days, twelve pots for each crop were separated into two groups. Two levels of nitrogen treatments, 5 and 30 ppm ^{14}N were applied to each group. After 38 days growing in these conditions, the nutrient solution containing 10 ppm ^{15}N double labeled $^{15}NH_4{}^{15}NO_3$ (10% atom excess) was applied to the 5 ppm ^{14}N group as low N treatment and that of 60 ppm ^{15}N was added to the 30 ppm ^{14}N group as control treatment. At 6 days after feeding ^{15}N, the same concentration of ^{14}N as NH_4NO_3 were applied to those groups instead of ^{15}N as shown in Fig. 15.

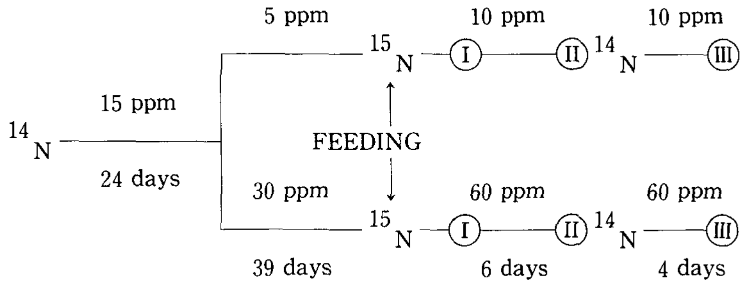

Fig. 15. Scheme of ^{15}N labeled experiment
I = First sampling (2 days after feeding ^{15}N).
II = Second sampling (6 days after feeding ^{15}N).
III = Third sampling (The end of 10 days ; 6 days after feeding with ^{15}N and 4 days with ^{14}N, consecutively).

Plant samples were collected three times during the experiment period, at 2 days and 6 days after feeding ^{15}N, and at the end of 10 days ; 6 days after feeding ^{15}N and 4 days after ^{14}N, consecutively. The samples were washed by deionized water, and separated into shoots, roots and tubers. These samples were dried at 80°C in an oven for 48 hours, weighed and analyzed.

The ^{15}N abundance in the Kjeldahl distillates was determined according to the Dumas techniques by emission spectrophotography using the JASCO NA-1 ^{15}N analyzer.

Results

Dry weight and total nitrogen content of sweet potato and potato increased gradually during the experimental period in the two N levels (Tables 16 and 17).

Nitrogen contents of both crops in the low N treatment were lower than the

Table 16. Dry weight of sweet potato and potato plants in the low N and the control treatments at different stages (g/pl).

	Low N			Control		
	I*	II*	III*	I	II	III
SWEET POTATO						
Shoots	3.43	3.92	3.89	4.29	4.64	5.41
Roots	0.75	0.89	0.96	0.89	0.84	1.09
Tubers	9.48	11.17	13.49	9.92	10.48	12.77
Total	13.66	15.98	18.34	15.10	15.96	19.27
POTATO						
Shoots	0.99	1.01	1.03	1.60	1.86	1.92
Roots	0.33	0.31	0.46	0.63	0.58	0.60
Tubers	5.36	7.10	8.68	8.88	8.91	10.69
Total	6.68	8.42	10.17	11.11	11.35	13.21

* I=2 days after feeding ^{15}N, II=6 days after feeding ^{15}N III=At the end of 10 days; after feeding 6 days with ^{15}N and 4 days with ^{14}N, consecutively.

Table 17. Nitrogen content (%)* of sweet potato and potato plants in the low N and the control treatments at different stages.

	Low N			control		
	I**	II	III	I	II	III
SWEET POTATO						
Shoots	1.42	1.71	1.94	2.91	2.86	3.36
Roots	1.06	1.18	1.11	2.06	2.14	2.09
Tubers	0.49	0.48	0.51	0.78	1.00	1.06
POTATO						
Shoots	1.88	2.29	2.52	2.82	3.16	3.74
Roots	1.50	1.98	2.18	1.97	2.58	2.45
Tubers	0.84	0.85	0.83	0.90	1.12	1.14

* $^{14}N+^{15}N$

** I=2 days after feeding ^{15}N, II=6 days after feeding ^{15}N III=At the end of 10 days; after feeding 6 days with ^{15}N and 4 days with ^{14}N, consecutively.

control. However, those of potato in the shoots, roots, and tubers were higher than those of sweet potato especially in the low N treatment.

^{15}N atom % excess (^{15}N abundance) in the roots and tubers of sweet potato at the I stage was higher than those of potato in both treatments (Table 18). ^{15}N abundance in the shoots was higher in potato than in sweet potato in the low N treatment. Opposite was true under the control treatment. At the II stage, except in the tubers of potato, those of sweet potato and potato in the all parts increased remarkably both in the low N and the control treatments. However, that of potato tubers was just slightly increased. That of sweet potato roots at the III stage declined strongly in both treatments. On the other hand, that of potato roots was not significantly changed at this stage. In sweet potato, those in the shoots and tubers were similar to the II sampling stage, whereas those of potato were slightly increased.

Table 18. ^{15}N abundance (% atom excess) in the plant of sweet potato and potato under the low N and the control treatments at different stages.

	Low N			Control		
	I*	II	III	I	II	III
SWEET POTATO						
Shoots	0.52	1.26	1.26	0.74	1.98	2.00
Roots	0.81	1.38	1.07	1.67	3.01	2.04
Tubers	0.54	1.17	1.08	0.81	1.37	1.61
POTATO						
Shoots	0.68	1.39	1.75	0.71	1.72	2.00
Roots	0.49	0.80	0.90	0.52	1.27	1.21
Tubers	0.48	0.56	0.73	0.45	0.93	0.99

* I=2 days after feeding ^{15}N, II=6 days after feeding ^{15}N, III=At the end of 10 days; after feeding 6 days with ^{15}N and 4 days with ^{14}N, consecutively.

The highest ^{15}N abundances of sweet potato at the I, and the II stages were obtained in the roots in both treatments. Furthermore, at the III stage under the low N treatment that of potato was highest in the shoots, while at the control treatment those in the roots and shoots were similar. On the other hand, in potato the highest ^{15}N abundance was observed in the shoots in both treatments at all stages.

Under the low N treatment, content of ^{15}N in the plant of sweet potato at 2 days after feeding ^{15}N (the I sampling stage) was lower than those of potato in all plant parts (Fig. 16). On the contrary, those of sweet potato in the control treatment were higher than those of potato. At 6 days after feeding ^{15}N (the II stage), the ^{15}N content in the shoots of both crops increased considerably in both treatments. In the low N treatment, the increases in ^{15}N level of sweet potato in the roots and tubers were slightly higher than that of potato. On the other hand, the increase in the control treatment was similar in both crops. Furthermore, at the end of 10 days ; after feeding 6 days with ^{15}N and 4 days with ^{14}N (the III stage), ^{15}N content of sweet potato in the roots declined remarkably in both treatments. On the other hand, that of potato decreased in the control and increased in the low N treatment. However, those in the shoots of both crops at this stage still increased in both the treatments. The increase in value of those of potato was higher than those of sweet potato.

At the I stage, ^{15}N content in the roots of sweet potato was the highest among the plant parts in both treatments, but that in shoots became highest at the II stage under the low N treatment. On the other hand, that of potato in the shoots was highest in all stages.

Amounts of ^{15}N accumulated in the shoots, roots and tubers of sweet potato were higher than those of potato in both treatments and in all stages (Fig. 17). The increasing rate of ^{15}N from the I stage to the II stage was higher in sweet

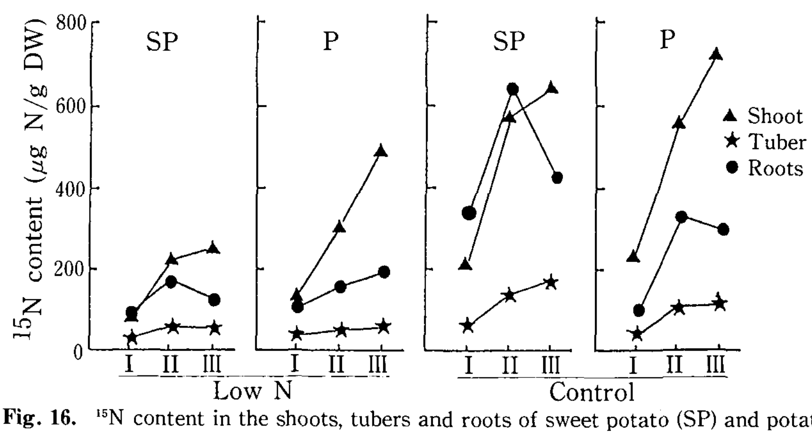

Fig. 16. ^{15}N content in the shoots, tubers and roots of sweet potato (SP) and potato (P) under the low N and the control treatments.
* I =2 days after feeding ^{15}N, II =6 days after feeding ^{15}N,
III=the end of 10 days ; after feeding 6 days with ^{15}N and 4 days with ^{14}N, consecutively.

potato than in potato. At the III stage, the amount of ^{15}N accumulated in the shoots of sweet potato in the low N treatment was quite similar to that at the II stage, but that of potato increased continuously. However, those of sweet potato and potato in the control treatment were similarly increased. The amount of ^{15}N accumulated at the I stage of sweet potato under the low N treatment was similar in the shoots and tubers, but that in the control treatment was highest in the shoots among the plant part. Those of potato were similar in the shoots and tubers and they were higher than those in the roots both in the low N and the control. It was observed at the II and the III stages that the larger amount of ^{15}N was translocated to the shoot in sweet potato than in potato.

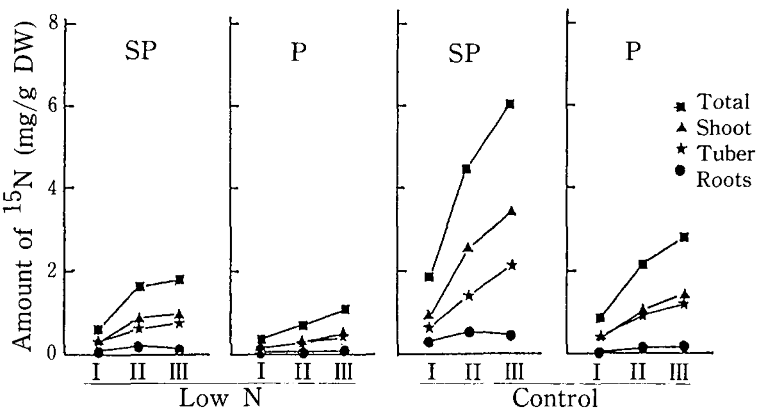

Fig. 17. Amount of ^{15}N accumulated in the shoots tubers, and roots of sweet potato (SP) and potato (P) under the low N and the control treatments.
* I =2 days after feeding ^{15}N, II =6 days after feeding ^{15}N,
III=the end of 10 days ; after feeding 6 days with ^{15}N and 4 days with ^{14}N, consecutively.

DISCUSSION

A. Tolerance to Low Nitrogen Conditions.

1) Dry matter production of sweet potato and potato.

Under field condition sweet potato var. Beniazuma was able to produce high tuber yield as well as potato var. Danshakuimo (Table 7). The highest yield obtained in the control treatment was 9.0 ton/ha in sweet potato while that of potato was 10.7 ton/ha. Thus, it was considered that sweet potato var. Beniazuma was reasonably well adapted to the cool temperature condition such as in Sapporo.

In the low nitrogen condition sweet potato produced larger relative total dry weight than that of potato in all growth media investigated, such as in the field (Figs. 2 and 9), water culture (Fig. 1), and vermiculite conditions (Table 16). Under water culture condition, the roots ability of sweet potato to grow and to elongate in the low nitrogen treatment was stronger than that of potato, and the relative dry weight of sweet potato roots was 5 times greater than that of potato

(Fig. 1). Relative tuber dry weight of sweet potato in the −N treatment was also higher than that of potato in all growth stages (Fig. 3). Difference between sweet potato and potato in the relative total and tuber dry weights in the −N treatment was greater at the early growth stage than at the later stages (Figs. 2 and 3). Furthermore, the relative tuber dry weight of sweet potato at the later stages was still twice greater than that of potato.

Based on the results mentioned above, it is suggested that tolerance of sweet potato to the low nitrogen condition is stronger than that of potato.

2) Mechanisms of different tolerance to the low nitrogen condition between sweet potato and potato.

The differences in the nitrogen absorbing power from the low nitrogen soils between sweet potato and potato is assumed as one of the important mechanisms of different tolerance to the low nitrogen conditions.

The total amount of nitrogen absorbed by sweet potato which was grown in the control treatment under water culture condition was remarkably higher and was more than three times larger than that of potato (Table 4). Under field condition, those of sweet potato were also larger than those of potato in both years (Tables 8 and 14) These phenomena indicated that nitrogen absorbing power of sweet potato was stronger than that of potato under the control treatment where nitrogen content in the growth media was sufficient.

Relative total amount of nitrogen absorbed by sweet potato from the low nitrogen treatment compared to the control treatment in the water culture experiment was also larger than that of potato (Table 4). Results obtained in the field experiment showed the similar tendency at the early growth stage (Table 8). However, the difference became smaller in the middle growth stage and at harvest. The reduction of the relative amount of nitrogen absorbed by sweet potato in the later growth stages might be caused by the decrease of inorganic nitrogen released from the soils. Thus, it could be assumed that absorbing power of sweet potato for nitrogen which is expressed by the relative total amount of nitrogen absorbed from the low nitrogen soil is far stronger than that of potato in the early growth stage, while it is stronger to some extent in the later stages.

The different characteristics of nitrogen absorbing power between sweet potato and potato as described above was clearly shown in the ^{15}N experiment where the total amounts of ^{15}N accumulated in the plant tissues of sweet potato at the three sampling stages were higher than those of potato in both treatments (Fig. 17).

The remarkably stronger nitrogen absorbing power of sweet potato than that of potato was observed under the low nitrogen condition in the water culture experiment. And it was considered to be caused by beneficial characteristics of sweet potato roots especially in the morphological mechanism. Under low nitrogen condition the relative length and the surface area of sweet potato root compared to the control treatment were 3-4 times higher than those of potato (Table 2).

It was suggested in this investigation that the capability of sweet potato and potato to translocate and to utilize nitrogen absorbed was different. Greater decrease in ^{15}N content in the roots of sweet potato during the II and the III stages than that of potato in the 10 and 60 ppm ^{15}N treatments evidenced that the translocation of nitrogen from roots to the shoots in sweet potato was faster than that of potato (Fig. 16).

Moreover, greater increase of ^{15}N abundance in the tuber of sweet potato at the II stage under the low ^{15}N treatment shows that the tubers of sweet potato is able to accumulate larger amount of nitrogen directly from roots than that of potato (Table 18). Since tubers of sweet potato is tuberous roots, it is assumed that amino acids produced from NH_4-nitrogen absorbed by roots were translocated from roots to tuberous roots and were assimilated there to protein. At the same time, other parts of nitrogen absorbed by roots translocated to the leaves. The ability of sweet potato tubers to accumulate nitrogen directly from the roots is considered to reduce their energy consumption. On the other hand, as a modification from stems, the tubers of potato have no connection with the roots directly. Therefore, the ability of potato tubers to accumulate nitrogen directly from roots was smaller than that of sweet potato.

In the low nitrogen soil condition, nitrogen content in the leaves, tubers and stems of sweet potato at the early growth stage were similar to those of potato, but it became lower than those of potato at the middle growth stage (Fig. 7 and Table 13). Thereafter, the nitrogen content in the leaves of sweet potato was maintained until harvest. On the other hand, that in the leaves of potato became drastically lower at harvest than that of sweet potato.

The leaf area index (LAI) and crop growth rate (CGR) patterns of sweet potato and potato were significantly different under the low N soil condition (Figs. 12 and 14). At the early stage, LAI of sweet potato was lower than that of potato, but it was gradually increased and they maintained until harvest. At 8 weeks after transplanting the LAI of sweet potato became higher than that of potato. On the contrary, the increase of leaf area of potato was rapid from the early growth stage, but drastically decreased at 11 weeks after emergence when the maturing period and shoot destruction started. Reflected to the LAI, CGR of sweet potato was lower at the early stage. At 11 weeks after transplanting, however, with drastic decrease of the CGR in potato, CGR of sweet potato became higher than that of potato until harvest. The lower CGR of sweet potato in the early stage might be due to the enhanced roots development under the low nitrogen condition.

Higher nitrogen content of potato tubers indicates that this plant has a strong sink power for nitrogen and this characteristic is considered to be related with the drastic decrease of nitrogen content in the leaves in the later growth stage. That is, the drastic decrease of nitrogen content in the potato leaves during maturity was caused by retranslocation of nitrogen from leaves to the tubers.

Lower content of nitrogen in sweet potato tubers showed that the internal requirement of sweet potato tubers for nitrogen was lower than that of potato. This characteristic was closely related to the stronger tolerance of sweet potato to low nitrogen condition than that of potato. Furthermore, the sink power of tubers for nitrogen of sweet potato was weaker than that of potato. Thus, nitrogen content in the leaves was maintained higher level than that of potato until harvest. In other words, since the internal requirement of potato tubers for nitrogen was higher than that of sweet potato, the nitrogen content in the leaves of potato became drastically lower during maturity and self-destruction of the leaves occurred. Furthermore, this self-destruction characteristic of potato was enhanced by the low nitrogen condition. On the other hand, in sweet potato, self-destruction did not occur and with relatively high LAI and nitrogen content in the leaves, sweet potato was able to maintain higher photosynthetic activity for longer duration even under the low nitrogen condition. It was, thus, considered that these characteristics of leaves also caused the stronger tolerance of sweet potato to the low nitrogen stress condition than that of potato.

Self-destruction of shoots during maturity is one advantageous characteristic of potato for the tuber enlargement since most of carbohydrate, protein and mineral nutrients accumulated in the leaves were translocated to the tubers. However, this characteristic of potato also became a factor limiting yield because leaves were destructed and growth duration became shorter. With the limited growth duration of potato caused by the self-destruction of leaves, various physiological activities such as photosynthesis had to be limited.

The longer growth duration and maintenance of relatively higher nitrogen content in the leaves until harvest in sweet potato are favorable characteristics for producing larger tuber dry matter under the low nitrogen condition.

The proportion of nitrogen accumulated in the roots of sweet potato at the early growth stage in the low nitrogen treatment under water culture condition was significantly greater than that of potato (Table 4). In respect to the higher proportion of nitrogen accumulated in the roots of sweet potato than that of potato it could be assumed that the capability of roots of sweet potato to utilize absorbed and assimilated NH_4-nitrogen directly for producing new roots was greater than those of potato. Thus, sweet potato was able to produce larger amount of roots than that of potato under the low nitrogen condition (Fig. 1). This physiological characteristic is also considered to be one of the important characteristics of sweet potato for the strong tolerance to low nitrogen condition.

In sweet potato, the proportion of tuber dry weight to the total dry weight under the low nitrogen condition in the later growth stage was higher than that under the control treatment especially at harvest (Fig. 6). In other words, the low nitrogen condition increased harvest index of sweet potato. Great increase of stem dry matter in sweet potato as a sink under the control treatment in the middle growth stage and at harvest reduced the amount of photosynthate translocated from leaves to tubers. However, under low nitrogen condition, proportion of the stem dry matter to the total dry matter became lower in sweet potato than that in the control treatment. By the low nitrogen soil condition, stem elongation of sweet pktato was considerably retarded. This morphological characteristic also becomes one of the mechanisms to attain the higher harvest index of sweet potato in the low nitrogen treatment than that in the control treatment (Fig. 6).

The proportion of tuber dry matter in the plant of potato at the middle growth stage in the low nitrogen treatment was lower than that in the control treatment (Fig. 6). Higher internal requirement of potato leaves for nitrogen and lower nitrogen supply from soil under the $-N$ treatment reduced the photosynthetic activity. Accordingly, the amount of photosynthate translocated to tubers was limited.

In potato grown in the low nitrogen treatment, the nitrogen use efficiency under the water culture condition and nitrogen efficiency under field condition in the low nitrogen treatment, were greater than those in sweet potato. However, the relative values of those in the low nitrogen condition compared to the control condition (100%) were higher in sweet potato than those of potato (Tables 5 and 10). The greater increase of the efficiency in sweet potato than in potato under the low nitrogen soil condition is considered to be caused by the lower nitrogen requirement of leaves and tubers in sweet potato than that of potato.

As a summary, it could be concluded that stroger tolerance of sweet potato to low nitrogen condition than that of potato was mainly due to (1) stronger nitrogen absorbing power ; the longer root elongation and longer growth duration are considered to be involved on the stronger absorbing power, (2) higher efficiency in translocation and utilization of nitrogen, (3) lower internal nitrogen requirement of leaves and tubers, (4) higher photosynthetic activity of leaves until harvest, and (5) the decrease in proportion of stems dry matter to the total dry matter in the low nitrogen condition.

In potato, the higher internal nitrogen requirement of leaves and tubers and self-destruction of shoot during maturity are unfavorable characteristics to tolerate low nitrogen condition.

B. Tolerance to Low Potassium Conditions.

The low potassium treatment strongly inhibited dry matter production and tuber yield of sweet potato and potato both in the water culture and the field conditions (Figs. 1, 4 and 5). However, the relative total dry weight of sweet potato compared to the control treatment under the field condition was comparatively higher than that of potato. At the early growth stage, the relative tuber dry weight of sweet potato was lower than that of potato, but at the middle growth stage and at harvest it became higher than that of potato. From above results, it is assumed that sweet potato had a slightly stronger tolerance to low potassium condition than that of potato.

Total amount of potassium absorbed by sweet potato at the early growth stage under water culture condition in the control treatment was considerably higher than that of potato (Table 4). In sweet potato, the relative amount of potassium absorbed in the −K treatment compared to the control treatment (100%) was slightly higher than that of potato at the early growth stage, but it became lower than that of potato in the later stages (Table 9). Thus, it is considered that the potassium absorbing power of potato under low potassium condition was slightly higher than that of sweet potato especially in the later growth stages.

The lower relative tuber dry weight of sweet potato at the early growth stage suggested that under the −K treatment, the limited amount of potassium absorbed was utilized primarily for producing larger amount of shoot. Thus, the tuber formation was rather inhibited. In the later stage, however, with the larger amount of leaves, sweet potato was able to produce greater photosynthates than potato and was able to translocate to the tubers. As a result, the tuber dry weight of sweet potato at the middle growth stage and at harvest became higher than those of potato.

Potassium content in the tubers of sweet potato was lower both in the low potassium and the control treatments than those of potato (Fig. 8). Thus, it indicates that the internal requirements of tubers for potassium were lower in sweet potato than in potato. Although, potassium content in the leaves under the −K treatment was similarly low in both plants, with the decrease of potassium content in the leaves, potato growth was poorer than that of sweet potato. The higher internal requirement of tubers in potato might also limit the tuber yield. These characteristics are considered to be most important factor for relatively stronger tolerance to low potassium condition in sweet potato than in potato.

As a summary, even the growth of both crops were strongly inhibited by the low potassium condition, a relatively stronger tolerance of sweet potato to low potassium condition than that of potato was mainly caused by the lower internal requirement of tubers for potassium in sweet potato than in potato.

III. TOLERANCE TO LOW PHOSPHORUS SOILS AND THE MECHANISMS

This part has been already reported in the previous Journal of the Faculty of Agriculture Hokkaido University[3].

IV. TOLERANCE TO ACID SOILS WITH DIFFERENT PHOSPHORUS AVAILABILITY AND THE MECHANISMS

Experiment 1 : Effect of low pH on growth and nutrient status under water culture condition.

Materials and methods

Four uniform seedlings of each crop were transplanted in a plastic container containing 350 liter aerated nutrient solution. Two levels of solution pH (4.0 and 5.0) were established in the solutions by adding H_2SO_4 or NaOH. During the experiment, the pH of the solutions was adjusted continuously with 0.1 N NaOH using an automatic pH regulator. Element concentrations (ppm) in all nutrient solutions were 30 N (NH_4NO_3), 1 P (NaH_2PO_4), 30 K (KCl : K_2SO_4=1 : 1), 50 Ca ($CaCl_2$), 20 Mg ($MgSO_4$), 2 Fe ($FeSO_4$), 0.5 Mn ($MnSO_4$), 0.5 B (H_3BO_4), 0.2 Zn ($ZnSO_4$), 0.01 Cu ($CuSO_4$), and 0.005 Mo ($(NH_4)_6Mo_7O_{24}$).

At 20 days after transplanting, all plants were harvested and separated into leaves, stems (including petioles) and roots after washing with deionized water. Plant samples were dried at 80°C in an oven for 48 hours and weighed. Phosphorus content in the leaves was determined by molybdenum yellow method, K content with a flamephotometer, while Ca and Mg were determined with an atomic absorption spectrophotometer.

Results

Total dry weight of sweet potato was slightly greater at pH 4.0 than at pH 5.0, while that of potato was slightly larger at pH 5.0 (Table 19).

Contents of P, K, Ca, and Mg in the leaves were slightly lower at pH 4.0 than at pH 5.0 both in sweet potato and potato, although the growth was not affected by the decrease in element content in both crops.

Table 19. Effect of solution pH on growth and nutrient content in the leaves of sweet potato and potato at 20 days after transplanting.

Treatment	Dry weight (g/pl)				Leaves nutrient content (%)			
	Shoots	Roots	Total	(%)	P	K	Ca	Mg
SWEET POTATO								
pH 4.0	9.91	1.22	11.1	114	0.73	3.7	0.51	0.48
pH 5.0	8.68	1.02	9.7	100	0.83	4.2	0.54	0.49
POTATO								
pH 4.0	3.57	0.51	4.1	88	0.61	4.9	0.62	0.32
pH 5.0	4.03	0.60	4.6	100	0.73	5.0	0.73	0.34

Experiment 2 : Effect of high aluminum concentration on growth and mineral element absorption under water culture condition.

Materials and methods

With similar procedure described in Experiment 1, four levels of aluminum concentration : 0, 2, 6, and 10 ppm Al were set up at pH 4.0 with 2 ppm P. $AlCl_3 \cdot 6H_2O$ and NaH_2PO_4 were added in the solutions and the pH was adjusted by an automatic pH regulator. Aluminum and phosphorus concentrations of solutions were determined every 2 days and adjusted to attain the intended concentrations. After the equilibrium of aluminum and phosphorus concentrations was attained, the seedlings of each crop were transplanted in the solutions. All plants at 20 days after transplanting were harvested and were separated into leaves, stems and roots. Length, surface area and diameter of roots were measured. Plant samples were dried and weighed. Element contents, such as Al, P, K, Ca, Mg, and Fe were determined.

Results

The increase of aluminum concentration in nutrient solution reduced relative total dry weights of both crops (Fig. 18). The relative dry weight of sweet potato in the high aluminum treatments was lower than that of potato. Length and surface area of roots was strongly retarded by aluminum treatments in both crops

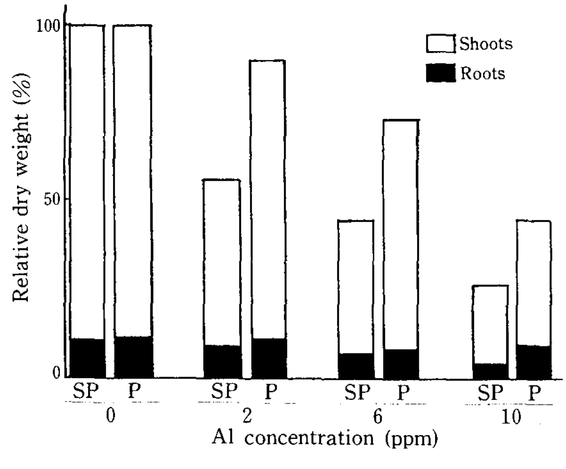

Fig. 18.
Effect of aluminum concentration on relative total dry weight of sweet potato (SP) and potato (P) at 20 days after transplanting under pH 4.0.

Table 20. Effect of aluminum concentration on root length, surface area, mean diameter of sweet potato and potato at 20 days after transplanting.

Aluminum concentration (ppm)	SWEET POTATO				POTATO			
	Root length		Surface area	Mean diameter	Root length		Surface area	Mean diameter
	(m/pl)	(%)	(m^2/pl)	(mm)	(m/pl)	(%)	(m^2/pl)	(mm)
0	247	100	0.45	0.58	93	100	0.14	0.46
2	119	48	0.25	0.66	57	61	0.11	0.61
6	82	33	0.18	0.70	38	41	0.08	0.65
10	52	22	0.11	0.65	36	38	0.08	0.72

Table 21. Effect of Aluminum concentration on element content in the plant tissues of sweet potato and potato under pH 4.0 at 20 days after transplanting.

Aluminum concentration (ppm)	Al (ppm)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (ppm)
			SWEET POTATO			
Leaves						
0	156	0.73	3.70	0.51	0.48	229
2	255	0.92	4.20	0.79	0.48	234
6	312	0.42	3.80	0.79	0.37	108
10	405	0.47	3.70	0.88	0.37	54
Stems						
0	98	0.62	5.90	0.96	0.44	486
2	138	0.69	5.70	1.04	0.45	230
6	150	0.41	5.20	0.91	0.39	190
10	178	0.42	4.10	0.61	0.36	149
Roots						
0	143	0.93	5.60	0.41	0.25	1340
2	1338	0.93	4.70	0.45	0.17	513
6	1889	0.65	3.90	0.40	0.16	340
10	3069	0.58	3.30	0.38	0.11	89
			POTATO			
Leaves						
0	210	0.61	4.90	0.62	0.32	219
2	249	0.79	4.40	0.86	0.49	161
6	270	0.45	4.30	0.72	0.34	180
10	331	0.42	4.10	0.61	0.36	149
Stems						
0	118	0.87	8.90	0.58	0.22	361
2	173	0.70	8.70	0.78	0.30	356
6	205	0.37	8.00	0.43	0.20	273
10	357	0.29	6.70	0.76	0.23	225
Roots						
0	511	1.48	3.70	0.31	0.23	2876
2	2643	1.35	4.30	0.30	0.31	825
6	4349	0.74	3.60	0.21	0.24	765
10	5259	0.57	3.10	0.25	0.24	859

(Table 20). On the contrary, mean diameter of roots in both crops was remarkably increased by aluminum treatments. The root length and surface area of sweet potato, however, were more inhibited by aluminum than those of potato. Aluminum toxicity symptom of roots such as dark brown color and thickened root tips was observed in sweet potato at 2, 6 and 10 ppm Al, while it was not observed in potato at 2 ppm Al treatments. The increase of aluminum concentration increased aluminum content in the leaves and roots of both crops (Table 21). On the contrary, P, K, and Fe contents were decreased. At 10 ppm Al *treatment, however, the contents of P, K, Ca, and Mg were not critical levels for* the deficiency in both crops. Magnesium content in sweet potato was decreased by aluminum treatments, but that of potato was not significantly affected.

Tremendously decreased Fe content in the leaves of sweet potato at high aluminum treatment induced Fe deficiency symptom such as pale yellow color in young leaves. That symptom did not appear in potato leaves.

Experiment 3 : Effect of low pH-high aluminum-low phosphorus traetment on growth and nutrient absorption under field condition.

Materials and methods

Sweet potato and potato were grown in an acid soil of experimental field of Hokkaido University in 1988. The size of each plot was 7.6 m×6 m, and each treatment was duplicated. Six combination treatments of three levels of soil pH (L_1, L_2 and L_3) and two levels of phosphorus application, without phosphorus (P_0) and 150 kg P_2O_5/ha (P_1) were given to those crops. In the P_0 treatment, only nitrogen and potassium have been applied for 10 years, while 150 kg P_2O_5/ha as superphosphate have been applied in the P_1 treatment. All treatments were fertilized with 100 kg N/ha and 100 kg K_2O/ha as ammonium sulfate and potassium sulfate, respectively. Top soils were collected from all treatments right before fertilizer application and the pH, avail. P_2O_5 (Bray II), exchangeable cation and CEC of soils were determined. Top soils were also collected at 40 day after planting in order to determine pH, Al, P, Ca, and Mn of soil solution.

From planting time to June 29, sweet potato was covered by transparent vinyl on the surface of soils. Plant samples were collected twice, at the middle growth stage and at harvest. Plant samples were separated into leaves, stems (including petioles) and tubers, dried at 80°C in an oven for 48 hours and weighed. Contents of Al, P, K, Ca, Mg, and Mn in the leaves of sweet potato and potato were determined at the middle growth stage. In this stage, root distributions were observed in the low pH (L_0-P_1), the low phosphorus (L_2-P_0), and the control (L_2-P_1) treatments.

Results

Exchangeable aluminum at the L_0 treatment was moderately high, 4.5 to 5.0 me/100 g (Table 22). Increasing soil pH reduced exchangeable aluminum and it was trace at the L_2 treatment. Available P_2O_5 determined by Bray II method was 5.2 to 6.2 mg and 10.7 to 11.3 mg P_2O_5/100 g at the P_0 and P_1 treatments, respectively.

The pH of the soil solutions collected at 40 days after planting was lower than that determined before fertilization (Table 23). Aluminum concentrations of the soil solution were slightly higher at the P_1 than at the P_0 treatments. On the other hand, concentrations of manganese in the soil solution at the L_0 treat-

Table 22. Chemical properties of soils before fertilizer application in 1988.

Treatment	pH		Avail.*	Exch. Cation (meq/100g)				CEC
	H_2O (1:2.5)	KCl (1:2.5)	P_2O_5 (mg/100g)	Al	K	Ca	Mg	(meq/100g)
L_0-P_0	4.90	3.44	6.19	5.0	1.07	9.7	1.06	28.8
L_0-P_1	4.98	3.45	11.05	4.5	1.01	10.9	1.01	
L_1-P_0	5.10	3.60	5.81	2.7	1.01	12.8	1.82	31.4
L_1-P_1	5.10	3.60	11.29	2.5	0.84	14.0	1.82	
L_2-P_0	6.20	4.58	5.20	trace	0.90	20.2	3.45	33.8
L_2-P_1	6.20	4.57	10.66	trace	0.81	21.6	3.52	

* Bray II method

Table 23. pH and concentration of Al, P, Ca, and Mn in the soil solution at 40 days after planting.

Treatment	pH	Al (ppm)	P (ppm)	Ca (ppm)	Mn (ppm)
L_0-P_0	4.12	3.7	0.05	193	1.7
L_0-P_1	4.04	5.7	0.07	255	1.6
L_1-P_0	4.45	1.8	0.04	242	1.0
L_1-P_1	4.25	2.5	0.09	301	1.4
L_2-P_0	5.01	trace	0.04	271	0.1
L_2-P_1	5.11	trace	0.12	341	0.1

Table 24. Effect of low pH and phosphorus treatments on dry weight of sweet potato and potato at the middle growth stage and at harvest(kg/ha).

	Middle growth stage				Harvest		
	Leaves	Stems	Tubers	Total	Shoots	Tubers	Total
SWEET POTATO							
L_0-P_0	1777	1985	2162	5924	3868	3983	7851
L_0-P_1	2023	2079	2959	7062	4886	5385	10271
L_1-P_0	2065	2192	2299	6556	4677	4348	9025
L_1-P_1	2275	2439	4026	8740	4710	6014	10724
L_2-P_0	1860	2271	3091	7222	5365	6634	11999
L_2-P_1	2643	2757	4076	9477	5227	6946	12173
POTATO							
L_0-P_0	484	325	1293	2101	188*	3931	4119
L_0-P_1	787	710	2151	3647	703*	6817	7520
L_1-P_0	557	347	1480	2383	524*	4818	5342
L_1-P_1	799	677	2437	3912	873*	7068	7941
L_2-P_0	741	510	1628	2879	638*	6176	6814
L_2-P_1	793	546	2442	3781	932*	7090	8022

* Dead shoots

ment were 1.6-1.7 ppm.

The highest yield of sweet potato and potato was obtained in the L_2-P_1 treatment. They were 6.9 and 7.1 ton DW/ha, respectively (Table 24). The relative dry weight was calculated on the basis of the total or tuber dry weight

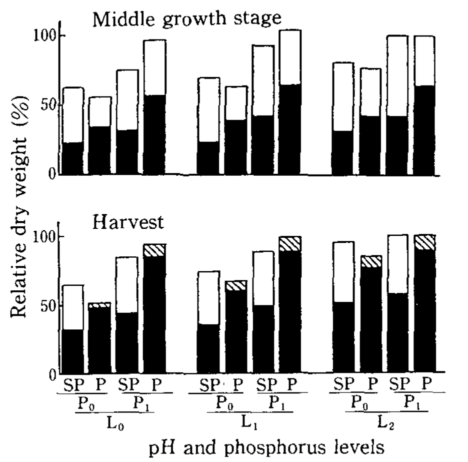

Fig. 19. Effect low of pH and phosphorus treatments on relative dry weight of sweet potato (SP) and potato (P) at the middle growth stage and at harvest.
☐ shoots ■ Tubers ▨ Dead shoots

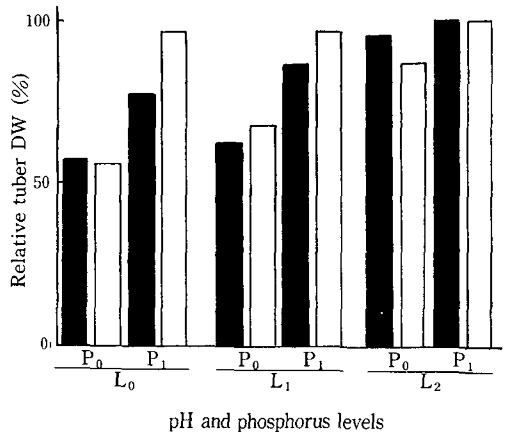

Fig. 20. Effect of low pH and phosphorus treatments on relative tuber dry weight of sweet potato ■ and potato ☐ at harvest.

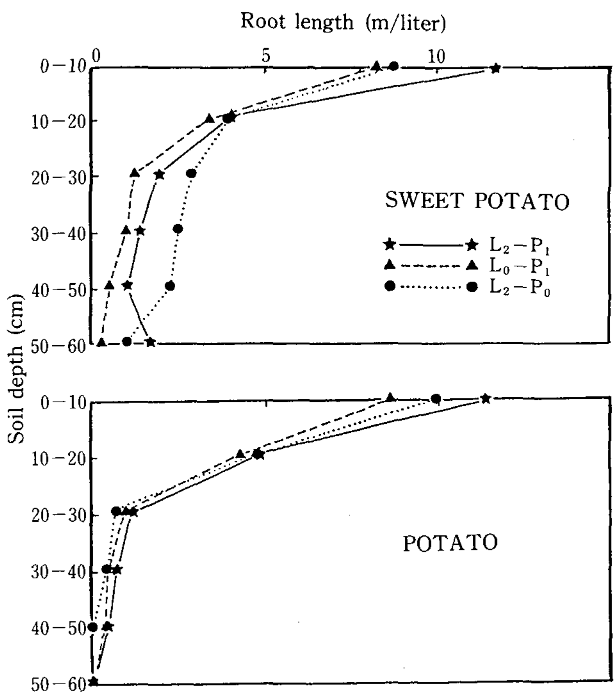

Fig. 21. Root distribution of sweet potato and potato indifferent soil depth in the low pH (L_0-P_1), the low phosphorus (L_2-P_0), and the control (L_2-P_1) treatments at the middle growth stage.

in the L_2-P_1 treatment (100%). At the L_0 and the L_1 treatments with phosphorus application, where pH was lower and the aluminum concentration was higher than the L_2P_1 treatment, the relative total and tuber dry weights of sweet potato were lower than those of potato (Figs. 19 and 20). On the other hand, the relative dry weights of potato were lower in the low pH without phosphorus application treatments than those of sweet potato. In the low pH and low phosphorus treatment (L_0-P_0), the relative tuber dry weight of sweet potato and potato was low and similar.

At the L_0-P_1 treatment, root elongation of both crops was inhibited, but the degree of inhibition in sweet potato was greater than in potato (Fig. 21).

Soil pH and phosphorus treatments affected the phosphorus content in plant tissues of both crops (Table 25). Low pH treatment reduced phosphorus content in the shoots of sweet potato and potato, especially at the middle growth stage. The phosphorus application increased phosphorus content both in shoots and tubers in both crops. However, the increasing rates of phosphorus content by phosphorus application in sweet potato was higher than that of potato.

Total amount of phosphorus absorbed by plant increased with the increase of soil pH and phosphorus application in both stages (Table 26). At the middle growth stage, total amount of phosphorus absorbed by sweet potato was larger than that of potato. While at harvest, the phosphorus accumulated in the tubers of potato was strongly increased and was higher than that of sweet potato. On the other hand, that of potato in shoots was drastically decreased.

Relationships between total phosphorus absorbed and total dry matter production are presented in Fig. 22. The relationships in sweet potato and potato were significant respectively both at the middle growth stage and at harvest.

Table 25. Effect of low pH and phosphorus treatments on phosphorus content (%) in the leaves, stems and tubers of sweet potato and potato at the middle growth stage and at harvest.

	Middle growth stage			Harvest			
	Leaves	Stems	Tubers	Leaves	Stems	Shoots*	Tubers
SWEET POTATO							
L_0-P_0	0.23	0.12	0.14	0.23	0.13	—	0.10
L_0-P_1	0.26	0.14	0.14	0.25	0.15	—	0.11
L_1-P_0	0.24	0.14	0.14	0.21	0.13	—	0.10
L_1-P_1	0.26	0.15	0.15	0.22	0.13	—	0.12
L_2-P_0	0.26	0.13	0.12	0.23	0.14	—	0.09
L_2-P_1	0.27	0.16	0.15	0.26	0.16	—	0.11
POTATO							
L_0-P_0	0.21	0.10	0.15	—	—	0.06	0.12
L_0-P_1	0.22	0.12	0.16	—	—	0.05	0.13
L_1-P_0	0.19	0.12	0.14	—	—	0.06	0.13
L_1-P_1	0.20	0.12	0.14	—	—	0.06	0.13
L_2-P_0	0.25	0.14	0.17	—	—	0.09	0.15
L_2-P_1	0.24	0.14	0.18	—	—	0.08	0.15

* Dead shoots

Table 26. Effect of low pH and phosphorus treatments on the amount of phosphorus absorbed by sweet potato and potato at the middle growth stage and at harvest (kg/ha).

	Middle growth stage				Harvest		
	Leaves	Stems	Tubers	Total	Shoots	Tubers	Total
SWEET POTATO							
L_0-P_0	4.23	2.41	3.02	9.7	7.01	3.98	11.0
L_0-P_1	5.20	2.97	4.14	12.3	9.74	5.92	15.7
L_1-P_0	4.98	3.05	3.22	11.3	7.90	4.35	12.3
L_1-P_1	5.85	3.73	6.53	16.1	8.47	7.22	15.7
L_2-P_0	5.11	3.21	3.57	11.9	10.19	5.97	16.2
L_2-P_1	7.22	4.41	6.11	17.7	11.00	7.64	18.6
POTATO							
L_0-P_0	0.98	0.33	1.93	3.23	0.11	4.72	4.83
L_0-P_1	1.64	0.82	3.01	5.47	0.35	8.86	9.21
L_1-P_0	0.95	0.39	2.20	3.53	0.31	6.26	6.57
L_1-P_1	1.59	0.77	3.54	5.90	0.52	9.19	9.71
L_2-P_0	1.86	0.71	2.93	5.50	0.57	9.26	9.83
L_2-P_1	1.90	0.75	4.11	6.76	0.74	10.64	11.38

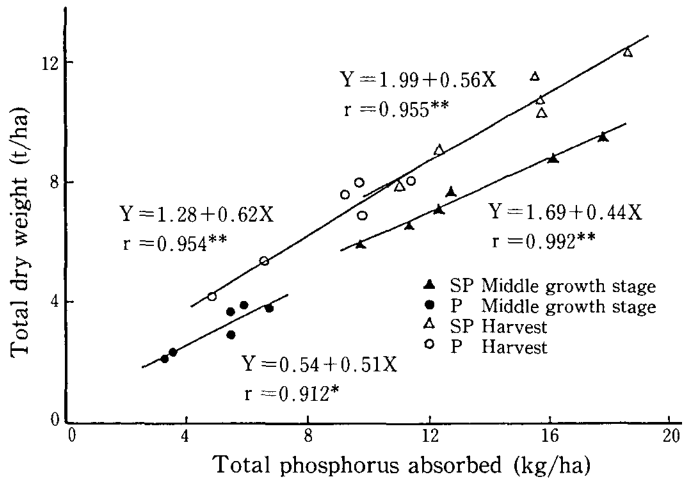

Fig. 22. Relationship betweeo total phosphorus absorbed and total dry weight of sweet potato (SP) and potato (P) at the middle growth stage and at harvest.

Table 27. Effect of low pH and phosphorus treatments on phosphorus efficiency of sweet potato and potato at harvest.

Treatment	SWEET POTATO		POTATO	
	((g DW/g P)*	(%)	(g DW/g P)	(%)
L_0-P_0	362	97	814	131
L_0-P_1	343	92	740	119
L_1-P_0	353	95	733	118
L_1-P_1	383	103	728	117
L_2-P_0	428	115	628	101
L_2-P_1	373	100	623	100

* g tuber DW/g phosphorus absorbed

The effect of low pH on phosphorus efficiency varied in both crops (Table 27), Phosphorus efficiency of sweet potato was lower than that of potato. That of sweet potato in the L_2-P_0 treatment increased compared with that in the L_2-P_1 treatment. This increase was higher than that in potato. However, those of sweet potato became lower in L_0 and L_1 than that in L_2 while those of potato became higher in the L_0 and L_1 than that in L_2.

Discussion

The low pH itself as low as 4.0 under water culture condition was not a limiting factor on growth of both crops (Table 19). Thus, it is considered that the poor growth obtained in the low pH treatment of field experiment, where pH of the soil solution was 4.0-4.3 was not caused by the effect of low pH itself.

Manganese concentration in the soil solution of the low pH treatment under field experiment ranged from 1.6-1.7 ppm (Table 23). These levels are far lower than the critical concentration for the toxicity[24]. It was indicated in the water culture experiment that growth of sweet potato was inhibited strongly and that of potato slightly by aluminum even at 2 ppm aluminum (Fig. 18). The aluminum concentration in the soil solution of the L_0 treatment ranged from 3.7-5.7 ppm (Table 23). The relative total and tuber dry weights of potato under the high aluminum soil condition (L_0-P_1 treatment) were greater than those of sweet potato both at the middle growth stage and at harvest (Figs 19 and 20). Thus, the poor growth obtained in the L_0-P_1 and L_1-P_1 treatments was mainly caused by aluminum toxicity. In other words, tolerance of potato to aluminum toxicity was stronger than that of sweet potato.

Stronger tolerance of potato to aluminum toxicity was caused by a beneficial characteristics, such as the capability of roots to tolerate high aluminum concentration. Under water culture condition, root elongation of sweet potato was more inhibited by aluminum than that of potato (Table 20). It has been shown that inhibition of root elongation is the first symptom of aluminum toxicity[22].

Mineral nutrient contents in the plant tissue of both crops were reduced by aluminum toxicity (Table 21). However, the decreased degree of Mg content in the leaves and roots by aluminum treatments was greater in sweet potato than in potato. LEE[13] reported that the aluminum tolerance of potato varieties was associated with the ability of roots to absorb magnesium. Fe deficiency symptom occurred in the leaves of sweet potato which was grown in the nutrient solution with a high aluminum concentration, but did not appear in potato. It has been reported that aluminum induced Fe deficiency in an aluminum sensitive cultivars of wheat, but not in tolerant cultivars[6]. Moreover, ADAM[2] postulated that aluminum interfered Fe metabolism with reduction of Fe^{3+} to Fe^{2+} within the plant. In addition, it is possible that Fe absorption was reduced competitively by Al^{3+} at the absorption sites.

The growth retardation at low pH treatment without phosphorus application

(L_0-P_0) was much severe in potato than in sweet potato (Figs. 19). On the other hand, growth retardation of potato in the L_0-P_1 treatment was slight and that of sweet potato was much severe. Furthermore, the growth retardation of both crops in the L_2-P_0 treatment was not severe. Root elongation of both crops in the nutrient solution with the concentration higher than 2 ppm Al was inhibited, although the degree of the inhibition was much larger in sweet potato than in potato (Table 20). Thus, it is considered that the severe growth retardation obtained in the L_0-P_0 treatment was caused by a combination of a high aluminum and a low phosphorus level of the soils. With the shorter root length caused by aluminum toxicity, amount of phosphorus absorbed by crops had to be decreased (Table 26).

Internal requirement of leaves and tubers for phosphorus also caused the severe growth retardation in both crops. However, the internal requirement for phosphorus is higher in potato than in sweet potato which was already demonstrated[3]. The poorer growth of potato than that of sweet potato obtained in the L_0-P_0 treatment is thus considered to be due to the higher internal requirement of potato for phosphorus than that of sweet potato.

The low tuber dry weight of both crops in the L_0-P_0 treatment indicated that the tolerance of the two crops to low pH-high aluminum-low phosphorus soil conditions was weak and similar. However, if compared to other crops it was stronger than sugar beet and barley, and similar to kidney been and oat[22] Therefore, status or rank of tolerance of these two crops among many crops is considered to be intermediate or moderately strong.

Although the amount of available phosphorus and concentration of phosphorus in the soil solution in the treatment without phosphorus application were low and similar in all pH levels, growth retardation of both crops in the L_0-P_0 treatment was more severe than in the L_2-P_0 and the L_1-P_0 treatments. Therefore, it is demonstrated that the inhibition of root elongation induced by aluminum toxicity is more important factor to decrease phosphorus absorption by plants than decrease of phosphorus availability of soil under low pH soil conditions.

As a summary, it could be concluded as follows. (1) Growth of sweet potato and potato was not significantly affected by low pH itself as low as pH 4.0. Thus, it was indicated that tolerance of both crops to low pH itself as low as pH 4.0 was strong. (2) Tolerance of sweet potato to aluminum toxicity was weaker than that of potato. The weaker tolerance of sweet potato to high aluminum was mainly caused by the greater inhibition of root formation and root elongation than that of potato. (3) The lower capability of sweet potato to absorb Fe and inducing Fe deficiency symptom in the young leaves of sweet potato in the high aluminum condition is considered as an adverse characteristic of sweet potato inducing the weaker tolerance to high aluminum soils. (4) Tolerance of both crops to low pH-high aluminum-low phosphorus soils was weak and similar.

However, if is compared to other crops, both of sweet potato and potato are classified intermediate or moderately strong (5) The rather weak tolerance of sweet potato and potato to low pH-high aluminum-low phosphorus soils was caused by a combination of the different tolerances to aluminum toxicity and low phosphorus. Weak tolerance of sweet potato to low pH-high aluminum-low phosphorus soils was mainly due to weaker tolerance to high aluminum conditions. On the other hand, that of potato was mainly due to weaker tolerance to low phosphorus and partly due to moderately weaker tolerance to high aluminum conditions.

GENERAL DISCUSSION

1. NUTRIO-PHYSIOLOGICAL CHARACTERISTICS OF SWEET POTATO AND POTATO IN THE TOLERANCE TO LOW NUTRIENT AND LOW pH CONDITIONS.

Plants differ in their tolerance and in the mechanisms which control this tolerance to low mineral nutrient and acid soils. The tolerance of plant species to low nutrient and acid soils is controlled by genetic factors, therefore closely related to the physiological and morphological characteristics of the plant.

In general, the tolerant plant species are characterized by high mineral efficiency and by their ability to reduce the adverse effect of toxic elements. Accordingly, they are capable of growing and producing relatively high yields under suboptimal soil conditions.

Comparison of tolerance to low nitrogen, low potassium, low phosphorus, low pH and high aluminum conditions between sweet potato and potato have been investigated. And the differences on the mechanisms of the tolerances have been clarified on the basis of their nutrio-physiological characteristics.

A. Tolerance to low nitrogen.

The higher relative total and tuber dry weight of sweet potato under low nitrogen conditions than those of potato indicated that tolerance of sweet potato to low nitrogen conditions is stronger than that of potato (Figs. 2 and 3).

Under water culture conditions it was obtained that the total amount of nitrogen absorbed by sweet potato was much greater than that of potato in low nitrogen conditions (Table 4). Similar tendency was obtained in the $-N$ treatment under field conditions during the early growth stage (Table 8). The difference between two crops became smaller during the later growth stages. The reduction of amount of nitrogen absorbed by sweet potato in the later stages might be caused by a decrease of inorganic nitrogen released from the soils. As a whole, it was considered that the nitrogen absorbing power of sweet potato was stronger than that of potato.

Under water culture conditions, the ability of sweet potato roots to grow and to elongate under the stress of low nitrogen supply was considerably stronger than that of potato (Fig. 1 and Table 2). This advantageous morphological characteristic of sweet potato roots is considered to be involved in the stronger absorbing power for nitrogen.

A ^{15}N labeled experiment indicated that sweet potato's capability to translocate nitrogen from the roots to the shoot was greater than that of potato (Fig. 16). Moreover, it was observed that the ability of sweet potato to assimilate NH_4-N under low nitrogen conditions was greater than that of potato (Table 18).

The lower internal nitrogen requirement of sweet potato's leaves and tubers and longer growth duration than that of potato are also advantageous characteristics for tolerance to low nitrogen (Fig. 7 and Table 13). These characteristics maintain the relatively higher photosynthetic activity of sweet potato until harvest in low nitrogen soils. Such characteristics enable sweet potato to tolerate low nitrogen soil conditions.

It is considered that the decrease of the proportion of stem dry matter as a sink to the total dry matter of sweet potato in low nitrogen soil conditions is a characteristic that favours increasing tuber yield and increasing harvest index (Fig. 6). On the other hand, the higher nitrogen content of potato tuber indicates that the sink power of potato tuber to accumulate nitrogen is stronger than that of sweet potato and that this characteristic causes the drastic decrease of nitrogen in the leaves of potato during the later growth stages. The self-destruction of potato shoots therefore occurrs during maturity. During this stage, most of the carbohydrates, mineral nutrients and nitrogen compounds are retranslocated from the shoot, especially from the leaves to the tubers. This characteristic contributes to a higher harvest index in potato. On the other hand, this characteristic reduces the photosynthetic activities caused by the limited growth duration of leaves.

It was observed that great increase of the harvest index of sweet potato under low nitrogen conditions caused the nitrogen efficiency of sweet potato to become higher in low nitrogen soil conditions than in high nitrogen conditions (Tables 10 and 15).

Based on the above results it could be concluded that the stronger tolerance of sweet potato to low nitrogen soils is due to (1) stronger nitrogen absorbing power ; the longer root elongation and longer growth duration affect the stronger absorbing power ; (2) the lower internal requirement both in leaves and tubers for nitrogen ; (3) higher efficiency on the nitrogen translocation and utilization ; (4) decrease in proportion of stem dry matter to the total dry matter and (5) maintenance of relatively higher photosynthetic activity until harvest increased tuber yield. On the other hand, the higher internal requirement for nitrogen and self-destruction of shoots is considered as an unfavorable characteristic of potato to tolerate low nitrogen soils.

B. Tolerance to low potassium

The relative total dry weight and the relative tuber yields of sweet potato and potato were considerably decreased by low potassium condition (Figs. 4 and 5). Nevertheles, under these conditions sweet potato produced a relatively greater yield than that of potato. Thus, it could be assumed that the tolerance of sweet potato to low potassium soils is slightly stronger than that of potato.

The lower content of potassium in the tubers of sweet potato under field condition indicated that the internal requirement of sweet potato tubers for potassium was lower than that of potato (Fig. 8).

The potassium absorbing power of sweet potato which is expressed by the relative total amount of potassium absorbed from the low potassium soil condition was larger at the early growth stage than that of potato (Table 9). But it decreased in the later stages and became similar to that of potato. Thus, it is considered that the absorbing power for potassium is similar in both crops. Stronger absorbing power of sweet potato during the early stage was caused by a larger amount of roots produced as shown in the water culture experiment.

In conclusion, it could be stated that relatively stronger tolerance of sweet potato to low potassium soils is mainly caused by the lower internal requirement of sweet potato tubers for potassium than that of potato.

C. Tolerance to low phosphorus

Under conditions of optimum soil pH, the growth of sweet potato and potato were retarded by low phosphorus soil condition. In these soils, however, the relative total dry weight and relative tuber yield of sweet potato were higher to some extent than those of potato[3].

The stronger tolerance of sweet potato to low phosphorus soils was influenced by several beneficial characteristics of this crop. Higher capability of sweet potato roots to grow and elongate in the deeper soil horizons under low phosphorus soils was considered to be an important beneficial morphological mechanism for a stronger absorbing power from the low phosphorus soils. The higher mycorrhizal infection in sweet potato roots than in potato roots was also an favourable factor, because these fungi could enhance the amount of phosphorus absorbed from the low phosphorus soils. On the thher hand, the comparatively dense root hairs of the potato was a favorable characteristic for increasing phosphorus absorbing power this plant. As a result, the phosphorus absorbing power of sweet potato was slightly higher or similar to that of potato.

The lower internal phosphorus requirement of the tubers of sweet potato than that of potato was another important factor in the success of sweet potato. Accordingly sweet potato was able to maintain a higher phtsphorus stasus and photosynthetic activity in the leaves for a longer growth duration than potato even under the low phosphorus soil conditions. In potato, phosphorus efficiency was higher than that of sweet potato. One advantageous characteristics of potato for higher efficiency is its capacity to self-destruct the shoot during maturity which enhances the translocation of photosynthates from leaves to tuber being induced by strong sink power of the tuber. However, the self-destruchive characteristic itself also becomes an unfavourable characteristic for the tolerance to low phosphorus soils, since by the shortened growth duration, the photosynthetic activity of leaves is also limited and this limitation of photosynthetic activity becomes more severe under the phosphorus deficient condition. As a result, the increase of the phosphorus efficiency of sweet potato in the low phosphorus soil conditions compared to the high phosphorus soil conditions becomes higher than that of potato.

As a conclusion, it could be stated that the stronger tolerance of sweet potato to low phosphorus soils is mainly caused by the lower internal requirement of the tubers for phosphorus. As a result sweet potato is able to maintain higher phosphorus content and photosynthetic activity of leaves for longer growth duration. On the other hand, it is considered that (1) the comparatively higher internal requirement of leaves and tubers for phosphorus and (2) the self-destruction of shoots in potato make it less easy for this plant to tolerate low phosphorus conditions than sweet potato. The study on tolerance to low phosphorus soils has already been publised[3].

D. Tolerance to acid soils.

Growth response to acid soils between the two crops was also different and it was influenced by several factors such as low nutrients and an element toxicity. The water culture study indicated that a pH as low as 4.0 did not become factor limiting growth of sweet potato and potato (Table 19). The low concentration of manganese in the soil solution of the acid soil investigated indicated that the poor growth of the two crops was not caused by manganese toxicity (Table 23).

Under field condition, the relative total dry weight and relative tuber yield of sweet potato, which was grown in the acid soil with phosphorus application and with high concentration of aluminum, were lower than those of potato (Figs. 19 and 20). From water culture experiment, it was observed that growth and root elongation of sweet potato was retarded more severely by aluminum treatment than that of potato (Fig. 18 and Table 20). Thus, it was assumed that tolerance of sweet potato to high aluminum conditions is weaker than that of potato and that the lower dry matter production of both crops in the acid soil was mainly affected by the aluminum toxicity. It was also shown that the ability of sweet potato to absorb Fe was weaker than that of potato (Table 21), especially at high concentrations of aluminum. Iron deficiency symptoms had appeared in the young leaves of sweet potato.

It was shown that the tolerance of both crops to the low pH-high aluminum-low phosphoruws soil was rather weak. The rather weak tolerance of sweet potato and potato to a low pH-high aluminum-low phosphorus soil was caused by a combination of their different levels of tolerance to low aluminum toxicity and low phosphorus soils. It could be concluded that the moderately weaker tolerance of sweet potato to these soils was mainly due to weaker tolerance to high aluminum. On the other hand, the poor growth of potato was mainly due to weaker tolerance to low phosphorus, and was partly caused by a moderately weaker tolerance to high aluminum conditions.

2. PROPOSALS TO IMPROVE THE PRODUCTIVITY OF SWEET POTATO AND POTATO UNDER ADVERSE SOIL CONDITIONS.

In order to improve the productivity of crops planted in adverse soils, applications of the necessary amounts of fertilizer, lime, and other amendments are required. This technology is called a high-input soil management technology. On the other hand, attempts to attain a reasonable but not necessarily maximum yield with a limited amount of fertilizer and other soil amendments is stated a low-input soil management technology. It is an important approach to maximize the use efficiency of a purchased input with using improved species or varieties of crops that have strong tolerance to the adverse soils[16].

Because of many limiting socio-economic factors, it is difficult in most developing countries to employ high input technology. The second approach is therefore more favored as a good alternative means to improve the productivity of crops. In addition, since the application of large amount of fertilizers frequently leads to pollution to the environment, a limited amount of fertilizer materials have to be used most efficiently for crop production by using improved species or varieties that use nutrients efficiently.

Concerning to the management of the adverse soils with low input technology, selection of tolerant species or varieties within species to adverse soils, an increase in the mineral nutrient efficiency of the crop plants, and screening of the higher affinity of symbiotic microbial organisms to each plant are primarily important.

A. Improving the nutrio-physiological characteristics of plants for stronger tolerance to low nitrogen soils

Based on the previous investigation under low nitrogen conditions, it was assumed that tolerance of sweet potato to low nitrogen soils was stronger than that of potato. Nevertheless, the tolerance of sweet potato to low nitrogen soils was not very strong. If the tolerance levels of both crops were improved, higher productivity than at present variety would be attained in low nitrogen soils with a small amount of nitrogen application. When tolerance of sweet potato and potato to low nitrogen soils are improved, the beneficial characteristics for stronger tolerance of both crops is required to be improved.

For sweet potato, the beneficial characteristics to be improved should be emphasized on (1) the increasing nitrogen efficiency with increasing the harvest index and (2) improving the photosynthetic activity of leaves.

For potato, it can be emphasized on (1) increasing the capability to produce longer roots, (2) reducing the internal requirement for nitrogen, (3) attaining the longer growth duration and to delay the self-destruction of shoots, and (4) improving the efficiency of nitrogen translocation and the utilization.

However, supplying at least a minimum amount of nitrogen is necessary especially if the nitrogen level in the soil is critical. The estimation of minimum amount of fertilizer applied should be based on crop requirement and soil conditions.

B. Improving the nutrio-physiological characteristics of plant for stronger tolerance to low potassium soils

Improvement of the beneficial characteristics of both crops under the low potassium soils should be done for increasing the productivity.

For sweet potato, improvement of nutrio-physiological characteristics should be focused on (1) increasing the absorbing power for potassium, (2) lowering the internal requirement for potassium, and (3) improving the potassium efficiency with increasing harvest index.

For potato, it should be emphasized on (1) increasing the absorbing power with longer root elongation under low potassium conditions, (2) reducing internal requirement for potassium, (3) delaying the self-destruction to maintain photosynthetic activity of leaves for longer period, and (4) improving potassium efficiency.

Application of a minimum amount of potassium fertilizer is recommended if the potassium availability in the soil is critical.

C. Improving the nutrio-physiological characteristics of plant for stronger tolerance to low phosphorus soils

The experimental results obtained in the phosphorus soils indicate that improving productivity in sweet potato can be approached by improving the following characteristics : 1) increasing absorbing power by improving the length and density of root hairs and by increasing the high affinity of mycorrhizal strains for roots. 2) reducing the internal phosphorus requirement of the leaves, 3) increasing the phosphorus efficiency by increasing the harvest index.

To improve potato it should be emphasized on (1) increasing the absorbing power by improving the capability of root elongation and by selection for high affinity of mycorrhizal strains which are favorable for potato roots. (2) reducing the internal phosphorus requirement of the leaves and tubers, (3) attaining much longer growth duration by delaying the self-destruction of shoots.

A minimum amount phosphorus fertilizer should be applied if the phosphorus status in the soils is at a critical level.

D. Improving the nutrio-physiological characteristics of plant for stronger tolerance to acid soils

It was suggested that aluminum in the soil solution of acid soils is more harmful than other factors and that phosphorus deficiency frequently becomes a growth limiting factor in acid soil. Therefore, improving the productivity was emphasized primarily on the elimination of aluminum effects and tolerance to low phosphorus soil conditions. Improvement of the following characteristics should be emphasized in screening the varieties of sweet potato, (1) improving the tolerance to aluminum toxicity on root formation and elongation, (2) making stronger the ability to absorb nutrient such as phosphorus, iron and magnesium, and (3) improving the tolerance to low phosphorus soil conditions by improvement of plant characteristics as described in part C.

For potato, improving the following characteristics is recommended, especially (1) improving the tolerance to low phosphorus soils conditions by improvement of plant characteristics described in part C and (2) increasing the capability of root elongation under low pH-high aluminum.

Improvement of soil pH to some extent by liming is recommended if the aluminum concentration in the soils is critical.

E. Improving productivity of crops under low-input soil management technology.

Based on the results obtained in this investigation, it could be concluded that sweet potato is a more adaptable crop for low input soil management technology where nitrogen and phosphorus are the most important nutrients for crop production than that of potato. However, when sweet potato is cultivated in the low nutrient-acid soils, the application of optimum amount of potassium together with minimum amount of nitrogen and phosphorus and application of minimum amount of lime to eliminate aluminum toxicity are required. Furthermore, for screening tolerant varieties of sweet potato, improvement of the high aluminum and low potassium tolerances are primarily required. Improvement of the internal requirement for potassium is the most important factor necessary to improve low potassium tolerance.

SUMMARY

Nutrio-physiological characteristics in relation to the tolerance to low nutrient and low pH soils were compared between sweet potato and potato.

1. Differences of the tolerance to low nutrient and low pH soils between the two crops were as follows.

(A) Tolerance of sweet potato to low nitrogen soils was stronger than that of potato.

(B) Tolerance of sweet potato to low potassium condition was slightly stronger than that of potato.

(C) Tolerance of sweet potato to low phosphorus soils was stronger to some extent than that of potato.
(D) Tolerance of the two crops to low pH itself was strong and similar.
(E) Tolerance of sweet potato to aluminum toxicity was weaker than that of potato.
(F) Tolerance of the two crops to low pH-high aluminum-low phosphorus soils was moderately weak and similar.

2. In the mechanisms of the stronger tolerance of sweet potato to low nitrogen and low phosporus soils, low internal requirement of the tuberous roots for the both elements is the most important characteristics.
3. Moderately weak tolerance of sweet potato to the low pH-high aluminum-low phtsphorus soil was mainly due to rather weak tolerance to high aluminum. On the other hand, that of potato was mainly due to the weak tolerance to low phosphorus and was partly due to the moderately weak tolerance to high aluminum. Status or rank in the tolerance of these two crops among many crops to the low pH-high aluminum-low phosphorus soil was considered to be intermediate or moderately strong.
4. Sweet potato is a more adaptable crop than potato to low input soil management technology where nitrogen and phosphorus are the most important nutrient for crop production.
5. For cultivation of sweet potato in low nutrient-acid soils, application of optimum amount of potassium together with minimum amount of nitrogen and phosphorus and application of a minimum amount of lime to eliminate aluminum toxicity are required.
6. For screening of tolerant varieties of sweet potato, improvement of their tolerance to high aluminum and low potassium soil conditions are primarily proposed.

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