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THE INTERRELATIONSHIPS OF IRON AND POTASSIUM IN THE POTATO PLANT*)

by E. W. BOLLE-JONES **)

INTRODUCTION

Evidence that iron and potassium are interrelated in the metabolism of the potato plant has been provided by preliminary experiments described by Hewitt and Bolle-Jones[9]) who suggested that potassium may enhance iron utilisation and that iron may impede the translocation of potassium. It was planned in the following pot-sand-culture experiments to make a more detailed study of the significance of these interrelationships in the potato and to find how these relationships were affected by the presence of calcium carbonate and varying levels of phosphate supply.

In the first of these experiments, carried out in 1948, potato plants were grown at varying levels of iron and potassium supply in the presence or absence of calcium carbonate. It was found that increased potassium supply increased the concentration of iron in the tubers and laminae but depressed the phosphorus and increased the chlorophyll concentrations of the laminae. The presence of calcium carbonate did not affect the nature of the relationships which existed between iron and potassium.

The results suggested, as the simplest working hypothesis, that the ameliorative effect of potassium on iron deficiency chlorosis might be explained in terms of its depressive effect on phosphorus concentration which increased the "availability" of the iron present in the lamina. Accordingly a factorial experiment designed to include varying levels of iron, potassium and phosphate was carried out to investigate this hypothesis in 1949. It was concluded as a result of

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**) Present address Rubber Research Institute of Malaya.

this experiment that the ameliorative influence of increased potassium supply on iron deficiency chlorosis was partially due to the increased iron concentration of the laminae and partially to the increased efficiency of iron utilisation in chlorophyll formation. This increased efficiency was attributed not only to the decreased phosphorus concentration, *per se*, but also to the effect of potassium in reducing the ability of the phosphorus to immobilise the iron in the laminae.

Although increased potassium supply increased the concentration of iron in the roots, tubers and laminae it was not known whether a greater "absolute" amount of iron was taken into the plant. The effects observed may have been due to a redistribution of iron within the plant. A study of the relative concentrations of potassium in young and old laminae had also indicated that increased iron supply affected the distribution of potassium within the potato plant but it was not known whether it affected total potassium uptake. An experiment, carried out in 1950, was designed to obtain information on these points. In addition, preliminary investigations designed to test the theory that the role of potassium in mitigating the severity of iron deficiency was connected with its effect on the conversion of inorganic to organic phosphate and, possibly, to its influence on the formation of organic acids, were carried out in 1951.

The following account is a description of these experiments. Most of the incidental observations in the literature relevant to this study, have been cited elsewhere [9]).

EXPERIMENTAL

1. *Design of experiments*

In the 1948 experiment there were thirty-two treatments representing combinations of four levels of iron, four levels of potassium and two levels (with and without) of calcium carbonate. The iron and potassium levels were chosen to represent severe deficiency (Fe_1 and K_1), mild deficiency (Fe_2 and K_2), normal (Fe_3 and K_3) and luxury (Fe_4 and K_4) consumption. These concentrations are given in Table I. Each treatment received a supply of soluble calcium. In addition, one half of the pots (C_2 treatments) each received 50 g of "Analar" grade calcium carbonate which was well mixed with the sand (9½ kilograms per pot) prior to planting; treatments not receiving calcium carbonate were designated C_1. A certified Scotch seed tuber, variety Majestic, was planted in each pot on the 10th May 1948; each treatment was carried out in duplicate and each replicate consisted of four pots.

The 1949 experiment was designed to include three levels each of iron, potassium and phosphate which were chosen to represent deficiency (Fe_1, K_1 and P_1), normal (Fe_2, K_2 and P_2) and luxury (Fe_3, K_3 and P_3) consumption. The concentrations of these nutrients are given in Table I. Each of the 27 treatments was carried out in duplicate and each replicate contained eight pots in each of which a tuber (variety Majestic) was planted on the 25th of May, 1949.

TABLE I

Nutrient levels of iron (Fe), potassium (K), and phosphate (P), expressed as milligram-equivalents per litre											
	1948	1949	1950–51		1948	1949	1950–51		1948	1949	1950–51
Fe_1	0.0005	0.0024	approx. 0.0016	K_1	0.50	0.60	0.60	P_1	—	0.90	0.90
Fe_2	0.0075	0.0600	—	K_2	1.25	2.40	—	P_2	4.00	2.70	—
Fe_3	0.1125	1.50	1.00	K_3	3.12	9.60	9.60	P_3	—	8.10	8.10
Fe_4	1.6875	—	—	K_4	7.81	—	—		—	—	—

In the 1950 experiment iron, potassium and phosphate were each applied at two levels chosen to represent deficiency (Fe_1, K_1 and P_1) and luxury consumption (Fe_3, K_3 and P_3). The potassium and phosphate levels were identical with those of the 1949 experiment (Table I). There were eight replicates, one in each block; each replicate or plot consisted of four pots. A tuber, variety Majestic, was carefully washed, dried and weighed before planting in each pot on the 2nd of May 1950.

In 1951 a few selected treatments, chosen so as to reproduce some of the main visual effects observed in the previous experiments of this series, were applied with or without the addition of organic acids to the nutrients. The acids chosen (malic, citric and oxalic) were applied at a concentration of 10 me/l.

Throughout these experiments calcium, magnesium and nitrate concentrations were maintained constant at 8, 3 and 12–14 me/l respectively; the supply of known micronutrients to each treatment was also constant.

2. *Culture technique*

Bitumen painted pots, acid washed sand, demineralised water and nutrients as described by Hewitt [7]) were used. There was no evidence to show that increased potassium level carried iron, as an impurity, into the nutrient. This point is one of considerable importance in the assessment of the experimental results. The pH of the nutrient solution increased with iron level; hence at deficiency levels of iron the nutrient pH hindered rather than favoured the production of chlorosis.

3. *Sampling and analytical procedures*

i. Sampling. "Young" and "old" (Hewitt and Bolle-Jones[9]) leaflets were sampled throughout each season at monthly intervals. The midrib was excised from each lamina and discarded; the following weights of lamina were then rapidly weighed out: 0.5 g (dry weight); 0.5 g (chlorophyll); 1.0–3.0 g ("soluble" K, P, and Ca) and 0.5–2.0 g ("soluble" Fe). Samples for dry weight were oven-dried at 85°C for 36 hours and reweighed; samples for chlorophyll estimation were stored in solid carbon dioxide. Samples for "soluble", nutrient estimations were stored at 5°C. The laminae which remained after this apportionment were dried and used for the determination of total nutrient elements. New tubers were analysed for the 1948–1950 experiments as well as the roots of the 1949 and 1950 plants.

In the 1950 experiment all plants grown in two of the Blocks (7 and 8) were completely harvested on the 11th of June; another two Blocks (3 and 4) were similarly harvested on the 13th of July. Plants grown in Blocks 3, 4, 7 and 8 were not sampled during the growing period; any fallen leaves were carefully collected and added to the "bottom" region of the shoot at the time of harvest. The aerial shoots of each plant were, on harvesting, subdivided into three regions according to length:

(*a*) the *Top* region which constituted $^1/_5$,
(*b*) the *Middle* region — $^2/_5$,
(*c*) the *Bottom* region — which contributed the remaining $^2/_5$.

Each region was further separated into laminae and stems plus petioles prior to being oven-dried. The "young" laminae of the 1948–1951 monthly samplings, were taken from the top region whereas the "old" laminae were taken from areas which corresponded partly with the middle and partly with the bottom regions.

ii. Maceration. All lamina samples macerated for the 1948 experiment were ground with purified quartz sand in 50-ml pyrex beakers with small glass pestles, an extracting reagent being added before grinding. For subsequent experiments samples of soluble iron or chlorophyll determination were macerated in the presence of ground glass or carborundum by a mechanically-driven all-glass homogeniser; samples for soluble K, P and Ca estimation were macerated in the "N.I.R.D." homogeniser, manufactured by Nelco Ltd.

iii. Estimation of chlorophyll. Each sample was macerated with 85% (V/V) acetone in the presence of about 5 mg of calcium carbonate and the extract made up to 50 ml with the extractant. Colorimetric measurement was carried out with a Spekker Absorptiometer using red filters. The chlorophyll calibration curve was obtained by adapting the methods described by Comar and others [2] [3] [4].

iv. Determination of soluble K, P and Ca status. The term "soluble" is here used to describe that fraction of potassium phosphorus or calcium present in the lamina which was extracted by Morgan's reagent[14]. The term is used without reference to any specific metabolic activity. In the 1948 experiment 1 g of lamina was macerated with 20 ml of Morgan's reagent in the presence of 0.2 g of carbon. In later experiments 3 g of lamina were macerated with 30 ml of Morgan's reagent in the presence of 0.6 g of carbon. All filtrates were colourless. The methods of chemical estimation were those described by Nicholas [14]).

v. Soluble iron. The terms "soluble", "active" or "available" iron were first used by Oserkowsky [17]) to designate that fraction of the iron present in leaves which he considered to be active in chlorophyll formation. He found the active fraction to be more abundant in the green leaves than in the chlorotic ones, although the reverse may be true for the total amount of iron in the leaves.

The methods used to determine soluble iron were based on preliminary results obtained in 1947 when numerous reagents were used to extract iron from the petioles of chlorotic (iron deficient) and green leaves of tomato, clover and sugar beet. Two reagents consistently extracted differential amounts from green and chlorotic leaves: 0.1 *N* HCl saturated with ether and 1.72% glycerophosphoric acid. The first extracted more ferrous and less ferric iron from the green than from the chlorotic leaves while the glycerophosphoric acid extracted little, if any ferric iron either from green or chlorotic leaves.

The hydrochloric acid and ether reagents used were purified by distillation. The iron was removed from the glycerophosphoric acid either as thiocyanate in a 1 : 1 mixture of amyl alcohol and amyl acetate or as hydroxyquinolate in chloroform. All extracting reagents were adjusted to a pH of 1.0.

The laminae were washed in 0.02 *N* HCl and dried between sheets of blotting paper before maceration. Extracts for the 1948 experiment were prepared from 2 g of lamina and 20 ml of extracting reagent; these proportions were later changed to 1 or 2 g of lamina per 30 ml of reagent. The final extracts were evaporated, wet digested and the iron content estimated with α,α-dipyridyl.

vi. Estimation of total nutrient concentration. 20 ml of nitric and 2 ml of perchloric acids per gram of dry matter were used in the wet digestion; no sulphuric acid was added. The final digests were analysed for iron, potassium, phosphorus and calcium using methods previously described [9]). The values obtained for potassium, phosphorus and calcium in leaf material from the same treatment in different blocks were reasonably concordant but for iron the agreement between duplicate plots was generally less satisfactory.

4. *Presentation of results*

Most of the experiments to be described were based on a factorial design; it is therefore possible to present the data as condensed mean tables which show clearly the overall and interaction effects. Standard errors are included within each table. It has only been possible to summarize a few of the more important results but the complete numerical data are available for consul-

Long Ashton Research Station. In the account of the results an attempt has been made to describe the effects general to all the experiments. Where effects were noted only in one particular experiment the latter is then referred to.

RESULTS

1. *Visual observations*

In all the experiments iron deficiency chlorosis appeared a month after planting in the Fe_1K_1 plants; it appeared first in the C_2 and in the P_2 and P_3 treatments. (Plate I).

In the 1948 experiment chlorosis appeared, but with diminished severity as the iron level increased, in the following plants: Fe_1K_1-C_1 and C_2, Fe_1K_2-C_1 and C_2, $Fe_1K_3C_2$, Fe_2K_1-C_1 and C_2, Fe_2K_2-C_1 and C_2, $Fe_2K_3C_2$, $Fe_3K_1C_2$, $Fe_3K_2C_2$. The young leaves of the $Fe_1K_3C_1$, $Fe_1K_4C_1$, Fe_2K_3-C_1 and C_2, Fe_2K_4-C_1 and C_2, $Fe_3K_3C_2$ plants were green and the old leaves relatively paler, in contrast to the corresponding K_1 plants in which the apical leaves remained chlorotic. This change in the relative distribution of green colour ("Fe/K visual response", Plate II) previously noted by Hewitt and Bolle-Jones [9]) was thus confirmed. The type of iron deficiency chlorosis observed was similar for both C_1 and C_2 plants; the symptoms of the C_2 plants were generally more severe than the corresponding C_1.

In the 1949 experiments the "Fe/K visual response" was apparent in the $Fe_1K_3P_2$ and $Fe_1K_3P_3$ plants at the beginning of the season (Plate II) but later these plants became apically chlorotic. Iron deficiency chlorosis was confined to the Fe_1 plants and was observed in the P_2, P_3 and K_1P_1 treatments during the experiment. Increased amounts of phosphate consistently increased the severity of the chlorosis at the Fe_1 level (Plate III).

Potassium deficiency symptoms were observed three to five weeks after planting in the Fe_1K_1 plants in the 1948 experiment and in the $Fe_1K_1P_3$ plants of the 1949–1951 experiments; symptoms did not appear in the corresponding high iron plants until a week later (Plate IV). At any one potassium level the appearance of potassium deficiency was delayed by an increase in the iron level of the nutrient (Plate IV). Potassium deficiency symptoms, which were apparent at the K_1 and K_2 levels only, were more severe in the C_2 plants and at the higher phosphate levels. Potassium deficiency at low iron levels was accompanied by continued apical growth and a marked defoliation of the lower region of the plant. At the higher iron levels, however, the symptoms were more drastic; they spread to the youngest leaves and caused the collapse and withering of the plant (Plate V).

Thus the effect of iron in delaying the inception of potassium deficiency and increasing its ultimate severity (Hewitt and Bolle-Jones [9])) was fully confirmed.

Where phosphate was applied at the lowest level phosphorus deficiency symptoms were observed, six weeks after planting, in the Fe_3K_2 and Fe_3K_3 plants. These symptoms were more severe at the high iron, high potassium and low phosphorus levels and were observed in the following treatments (of the 1949 experiment):

$Fe_1K_2P_1$, $Fe_1K_3P_1$, $Fe_2K_2P_1$, $Fe_2K_3P_1$, $Fe_2K_3P_2$,
$Fe_3K_1P_1$, $Fe_3K_2P_1$, $Fe_3K_3P_1$, $Fe_3K_3P_2$.

It was interesting to note that the $Fe_3K_1P_1$ plants developed phosphorus deficiency symptoms while the $Fe_3K_1P_3$ and $Fe_1K_1P_1$ plants showed potassium deficiency symptoms.

Symptoms attributed to combined effects of calcium deficiency and low phosphorus status were observed fifteen weeks after planting in the 1948 experiment and usually 8–10 weeks after planting in the subsequent experiments. The laminae became reduced in size, the margins became wavy and inrolled towards the dorsal surface and a basal chlorosis appeared (Plate VI). The straplike leaflets withered from the tip downwards and turned a bright yellow; death of the leaflets followed but the stem growing point continued upwards producing elongated internodes and leaflets progressively reduced in size. Brown lesions appeared along the stem and the growing point was finally killed. In contrast to the rapid formation and pre-mature death of the young laminae, the old laminae retained their green colour and remained attached to the stem for long periods. In the 1948 experiment these symptoms occurred in both C_1 and C_2 series in the K_2, K_3 and K_4 plants at the Fe_3 and Fe_4 levels. The symptoms increased in severity with either iron or potassium level but were less severe where calcium carbonate had been added.

In the 1949 experiment these symptoms were first apparent in the $Fe_1K_3P_1$, $Fe_2K_3P_1$ and Fe_3K_3-P_1, P_2 and P_3 plants and hence appeared to be caused by the high potassium level (Plate VII). They were observed also in the $Fe_2K_2P_1$, Fe_2K_3-P_2 and P_3, and $Fe_3K_2P_1$ plants at a later date. In general the incidence and severity of these calcium-phosphorus deficiency symptoms increased with iron or potassium (Plate VII) or decreased phosphate, supplies.

In the 1951 experiment it was noted that the $Fe_1K_1P_1$ and $Fe_1K_1P_3$ plants supplied with oxalic acid showed a more severe iron deficiency chlorosis than those not supplied with acid; malic acid had a similar but much milder effect. The addition of citric acid did not increase the severity of these symptoms but neither did it alleviate their severity. An effect of organic acid addition on the occurrence or severity of potassium deficiency symptoms was not noted.

2. *The occurrence of tuber necrosis*

A close examination of the tubers produced by plants exhibiting calcium deficiency — low phosphorus effects in the shoot, revealed that small, malformed, corky tubers (described as calcium deficient by Hewitt [8]), and Wallace [36])) occurred sporadically in the higher potassium treatments. In addition two distinct types of tuber necrosis were observed and are described below, with special reference to the 1949 experiment.

(i) External necrosis. This originated at the "rose" end of the tuber. It was visible externally as a dry, brown, partially rotted region situated mainly in the cortex; sometimes it extended into and became continuous with a medullary necrosis, described below. No pathogen was detected and the occurrence did not exceed 15%. The external necrosis appeared in the K_3 treatments.

(ii) Medullary necrosis (Plate VIII). In numerous instances the central or medulla region of tubers, which appeared to be externally normal, was completely rotted. This breakdown originated in the central region of the tuber and was not necessarily connected to the "rose" end exterior. It began as numerous brown necrotic spots, close together in the middle of the medulla. These were small groups of cells the contents of which became granular and orange brown in colour. These cells later became disorganised, adjacent regions coalesced and ultimately broke down to form a brown cavity, later turning black. Medullary necrosis was always found in malformed calcium deficient tubers. The symptoms were not those of "Spraing", "Internal rust spot" or the "Net necrosis" reviewed by Quanjer [19]). The application of potassium increased while that of phosphorus decreased the occurrence of medullary necrosis;

Plate I. Potato plant given $Fe_1K_1P_3$ nutrient. Note intense apical chlorosis and necrotic veining of younger laminae and potassium deficiency in the old.

Plate II. Effect of potassium on iron deficiency. *Left:* Low Fe and high K nutrient. *Right:* Low Fe and low K nutrient. *Note:* apical iron deficiency chlorosis and severe potassium deficiency symptoms in low K plant; dark green young leaves and paler midstem leaves of high K plant.

Plate VII. Effects of potassium in inducing calcium deficiency symptoms associated with low posphorus status in young laminae. $Fe_1K_1P_1$ plant (*left*) : $Fe_1K_3P_1$ plant (*right*). *Note:* slight potassium deficiency in the old laminae of the K_1 plant; calcium deficiency in the young and phosphorus deficiency in the old leaves of the K_3 plant; changed habit of K_3 plant.

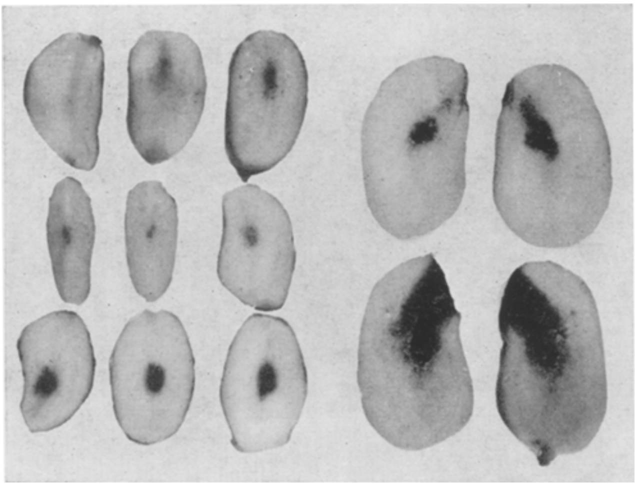

Plate VIII. *Left:* stages in development of medullary necrosis in tubers. *Right:* medullary necrosis becoming continuous with external necrosis.

these effects were highly significant (Table II). The effect of iron supply was complex; potassium supply was the determining factor.

TABLE II

Incidence of medullary necrosis. Means obtained by an angular transformation of the percentage values to illustrate the main effects and interactions. 1949 experiment

Treatment level	K_1	K_2	K_3	P_1	P_2	P_3	Mean
		(± 0.86)			(± 0.86)		(± 0.50)
Fe_1	5.6	8.7	24.4	19.2	11.4	8.2	12.9
Fe_2	11.1	13.0	28.4	21.8	17.4	13.1	17.5
Fe_3	8.5	13.4	22.9	15.8	16.97	12.1	14.9
P_1	9.8	13.9	33.1	—	—	—	18.9
P_2	9.5	13.6	22.8	—	—	—	15.3
P_3	5.9	7.7	19.8	—	—	—	11.2
Mean	8.4	11.7 (± 0.50)	25.2	—	—	—	15.1

3. *Yield data*

In general the effects of potassium and phosphate addition were to increase the dry weight yield of shoots, roots and tubers while calcium carbonate decreased both shoot and tuber yields. The ad-

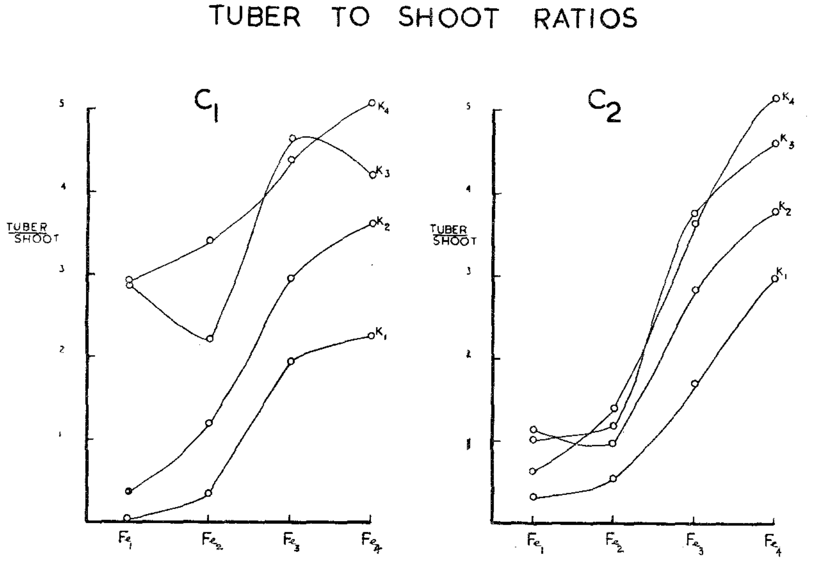

Fig. 1. Variation of dry weight ratio of tuber to shoot with iron level. 1948 experiment.

dition of iron reduced the dry weight of both shoots and roots but increased that of the tubers. This effect was reflected in the striking, and perhaps economically important, increase in the ratio of tuber to shoot which was obtained on the application of iron (Fig. 1).

The yield of tubers obtained in the 1948 experiment furnished a clear instance of the interrelationship which existed between iron and potassium (Table III). Thus addition of iron at the K_1 level caused a 11-fold increase in yield but had relatively little effect at the K_4 level; the response to potassium at the Fe_1 level was 27-fold as compared with a 2–3 fold increase in yield at the Fe_4 level.

TABLE III

Dry weight of tubers (grams per 4 plants). Mean values. 1948 experiment

Treatment level	Fe_1	Fe_2	Fe_3	Fe_4	C_1	C_2	Mean
K_1	13	54	151	144	90	91	90
K_2	73	172	314	289	224	199	212
		(± 29.8)			(± 21.0)		(± 14.9)
K_3	295	223	527	411	449	279	364
K_4	356	482	532	390	623	258	440
C_1	292	332	415	347			347
		(± 21.0)					(± 10.5)
C_2	76	134	347	270			207
Mean	184	233	381	308	347	207	277
		(± 14.9)			(± 10.5)		

Tubers, although small in weight and few in number, were present in the 1950 experiment when Blocks 7 and 8 were harvested; the yield rose sharply by the time Blocks 3 and 4 were harvested. The total dry weight of the complete plants (Table IV) increased with

TABLE IV

Total dry weight of complete plants. Blocks 3, 4, 7 and 8. (grams per 4 plants). Mean values. 1950 experiment

Month	S.E. horizontal comparison	Treatment level												S.E. vertical comparison
		Fe_1		Fe_3		K_1		K_3		P_1		P_3		
		K_1	K_3	K_1	K_3	P_1	P_3	P_1	P_3	Fe_1	Fe_3	Fe_1	Fe_3	
June Blocks 7 & 8	± 10.4	82	96	90	88	70	100	80	103	85	66	90	113	± 12.6
	± 7.3	89		89		85		92		76		102		± 8.9
July Blocks 3 & 4	± 10.4	161	266	165	229	154	172	196	300	206	144	222	250	± 12.6
	± 7.3	214		197		163		248		175		236		± 8.9

either potassium or phosphate application. The addition of iron decreased the yield at the P_1 but had no significant effect at the P_3 level.

The provision of organic acid supplements in the 1951 experiment did not enhance the total dry weight yield per plant. Citric acid did not have a detrimental effect whereas oxalic acid did and markedly reduced growth in the $Fe_1K_1P_3$ plants. Malic acid was equally deleterious when given to the same plants but where iron deficiency was not so severe or apparent (as in the $Fe_1K_1P_1$ and $Fe_1K_3P_3$ plants) it did not severely retard growth.

4. *Chemical data*

i. Chlorophyll concentration of the laminae (Table V). The application of iron increased the chlorophyll concentration of young and old laminae; this increase was greater at the lower potassium levels for the young laminae and at the higher phosphate levels for the old laminae.

TABLE V

Chlorophyll concentration of laminae expressed as mg per gram of dry matter
Means of all values for June, July and August 1949

Treatment level	Young laminae							Old laminae						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
		(± 0.23)			(± 0.23)		(± 0.14)		(± 0.28)			(± 0.28)		(± 0.16)
K_1	6.6	9.0	8.9	9.2	8.3	7.0	8.2	5.0	6.0	6.8	7.1	5.6	5.1	5.9
K_2	7.7	9.5	9.6	9.1	9.2	8.5	8.9	6.4	8.0	9.0	8.7	7.4	7.3	7.8
K_3	8.1	8.7	8.1	7.5	9.0	8.4	8.3	6.8	8.6	8.9	8.1	8.2	8.1	8.1
P_1	7.4	9.2	9.2	—	—	—	8.6	7.1	8.0	8.7	—	—	—	8.0
P_2	7.7	9.8	9.0	—	—	—	8.8	5.7	7.2	8.2	—	—	—	7.1
P_3	7.2	8.2	8.4	—	—	—	8.0	5.4	7.4	7.8	—	—	—	6.8
Mean	7.4	9.1	8.9	—	—	—	8.5	6.1	7.5	8.2	—	—	—	7.3
		(± 0.14)							(± 0.16)					

The addition of potassium increased the chlorophyll concentration of the old laminae at all iron levels and of the young laminae at the Fe_1 level, but caused a decrease at the higher iron levels. The response to potassium, in the 1948 experiment, was more pronounced for the C_1 than for the C_2 plants for both young and old laminae. In the subsequent experiments addition of potassium decreased the chlorophyll concentration of the young laminae at the P_1 level but increased it at the P_2 and especially at the P_3 levels. Increased potassium supply generally increased the chlorophyll content of the old laminae at all phosphate levels.

Calcium carbonate addition decreased the chlorophyll concentration of both young and old laminae and particularly so for the low iron treatments.

The application of phosphate reduced the chlorophyll concentration of both young and old laminae; this reduction was most marked at the K_1 level and least apparent at the K_3 level. The depressive influence of phosphate was greatest at the Fe_1 level in the old laminae.

It was noted, for the 1951 experiment, that organic acid addition did not generally increase the chlorophyll content of the laminae; in fact, oxalic acid addition markedly reduced the chlorophyll concentration, as also did malic acid to some extent.

ii. Titratable acidity. Representative values obtained for titratable acidity are summarised in Table VI. Increased potassium level decreased the acidity of the young laminae but either had little effect or increased that of the old laminae. Thus the increase which occurred in the chlorophyll concentration of the young laminae of the Fe_1P_3 plants when the potassium supply was increased was accompanied by a decrease in the titratable acidity. Phosphorus addition invariably increased the acidity of both young and old laminae. The influence of either iron or organic acid supplements was not consistent.

TABLE VI

Titratable acidity (Volume, ml of 0.01 *N* NaOH required to bring extract to pH 9.5)

Young laminae	1950	1951	Young laminae 1951						
$Fe_1K_1P_1$	8.2	7.6	Control	$Fe_1K_1P_1$	6.9	$Fe_1K_1P_3$	14.0	$Fe_1K_3P_3$	8.2
$Fe_1K_1P_3$	12.0	13.8	Malic	$Fe_1K_1P_1$	5.8	$Fe_1K_1P_3$	13.0	$Fe_1K_3P_3$	10.7
$Fe_1K_3P_3$	10.5	9.7	Citric	$Fe_1K_1P_1$	6.7	$Fe_1K_1P_3$	12.2	$Fe_1K_3P_3$	11.9
$Fe_3K_3P_3$	11.0	11.8	Oxalic	$Fe_1K_1P_1$	7.2	$Fe_1K_1P_3$	13.4	$Fe_1K_3P_3$	11.8
Old laminae	1950		Old laminae 1951						
$Fe_1K_1P_1$	6.0	—	Control	$Fe_1K_1P_1$	5.2	$Fe_1K_1P_3$	11.6	$Fe_1K_3P_3$	13.2
$Fe_1K_1P_3$	7.2	—	Malic	$Fe_1K_1P_1$	3.8	$Fe_1K_1P_3$	14.8	$Fe_1K_3P_3$	16.8
$Fe_1K_3P_3$	10.6	—	Citric	$Fe_1K_1P_1$	3.9	$Fe_1K_1P_3$	10.9	$Fe_1K_3P_3$	9.9
$Fe_3K_3P_3$	11.8	—	Oxalic	$Fe_1K_1P_1$	—	$Fe_1K_1P_3$	9.1	$Fe_1K_3P_3$	9.5

1950 extracts prepared by extracting 5 g fresh laminae with 60 ml of 85% alcohol; 1951 extracts prepared by taking 3 ml of sap expressed from fresh laminae and diluting with water to 25 ml before titration.

Samples of juice expressed from frozen laminae of plants grown in the 1951 experiment were examined chromatographically for organic acid constituents by Mr. A. H. Williams. None of the commoner acids was readily detected in the juice. One "unknown" acid only showed variation with mineral treatment; the amount of this acid present did not vary consistently as a result of the organic acids supplied in the nutrients. This "unknown" acid possessed an R_F value similar to malic acid when the chromatograms were run in an acid solvent (butanol-formic acid) but similar to lactic acid when run in an alkaline solvent (ethanol-ammonia). The "unknown" acid was always found in least concentration in juice taken from the $Fe_1K_1P_3$ laminae and in highest concentration in the $Fe_1K_3P_3$ laminae.

Apparently the organic acids fed to the plants either became localised in the roots, tubers or stems or were metabolised completely. In one instance only was there any indication that the plants had been fed with organic acids when a large genuine malic acid spot was obtained in the old laminae taken from $Fe_1K_3P_3$ plants fed with malic acid.

iii. Inorganic and organic phosphorus in laminae (Table VII). Fresh laminae were macerated with ice-cold 10% perchloric acid. The estimation of inorganic phosphorus in the supernatant liquid after centrifuging was based on procedures described by Weil-Malherbe and Green 38). The amount of organic phosphorus in the laminae was obtained by subtracting the inorganic phosphorus value from the total phosphorus value determined by the usual wet digestion procedure and subsequent colorimetric estimation.

TABLE VII

Inorganic and organic phosphorus concentrations of young laminae (expressed as mg P per gram dry matter). Mean values. 1951 experiment

Treatment	1st sampling					2nd sampling				
	Inorg. P	Org. P	$\frac{\text{Inorg.}}{\text{Total}}$	$\frac{\text{Org.}}{\text{Total}}$	$\frac{\text{Inorg.}}{\text{Org.}}$	Inorg. P	Org. P	$\frac{\text{Inorg.}}{\text{Total}}$	$\frac{\text{Org.}}{\text{Total}}$	$\frac{\text{Inorg.}}{\text{Org.}}$
$Fe_1K_1P_3$	7.11	1.88	.79	.21	3.78	6.23	6.23	.50	.50	1.00
$Fe_1K_2P_3$	5.54	1.56	.78	.22	3.55	3.99	5.88	.40	.60	0.68
$Fe_1K_3P_3$	1.90	2.05	.48	.52	0.93	2.12	4.59	.32	.68	0.46
$Fe_2K_2P_3$	4.28	2.00	.68	.32	2.14	5.16	4.26	.55	.45	1.21
$Fe_3K_3P_3$	3.72	3.02	.55	.45	1.23	3.33	4.19	.44	.56	0.80

The concentration of inorganic phosphorus and its proportion of the total phosphorus in the lamina, decreased as the potassium level of the nutrient increased. Potassium level did not usually affect the concentration of organic phosphorus present but increased its proportion of the total (*i.e.* organic P/total P). Increased potassium supplies markedly decreased the ratio value for inorganic/organic phosphorus found in the laminae.

Increased iron level generally increased the concentration and proportion of inorganic phosphorus present.

iv. Morgan's-soluble K, P and Ca (Table VIII). Increased iron supply decreased the soluble potassium concentration of the young laminae at the K_1 level but increased the potassium concentration of the old laminae at all K levels. The addition of calcium carbonate tended to increase the potassium concentration of the young laminae but significantly reduced that of the old laminae. Phosphate addition caused an overall decrease in the potassium concentration of the old laminae.

TABLE VIII

% Morgan's-soluble potassium, phosphorus and calcium in laminae, expressed on dry weight basis. Overall mean values. July sampling 1949

Treatment level	Young laminae			Old laminae		
	% K	% P	% Ca	% K	% P	% Ca
	(± .08)	(± .017)	(± .054)	(± .08)	(± .008)	(± .07)
Fe_1	2.1	.20	.50	1.5	.19	2.0
Fe_2	1.7	.13	.28	1.7	.13	1.7
Fe_3	1.8	.12	.55	2.0	.12	1.8
	(± .08)	(± .017)	(± .054)	(± .08)	(± .008)	(± .07)
K_1	1.3	.20	.60	0.4	.19	2.1
K_2	1.5	.15	.54	1.0	.16	2.4
K_3	2.8	.11	.19	3.8	.10	1.1
	(± .08)	(± .017)	(± .054)	(± .08)	(± .008)	(± .07)
P_1	1.8	.04	.44	2.0	.03	1.5
P_2	1.9	.12	.42	1.6	.07	2.0
P_3	1.9	.30	.47	1.5	.34	2.0

The addition of iron or potassium decreased the soluble phosphorus concentration of the young laminae; this also applied to the old laminae for the 1949 and subsequent experiments. The effects of both iron and potassium were most marked at the P_3 level. The addition of calcium carbonate decreased the phosphorus concentration of the old laminae.

The effect of iron level on soluble calcium concentration was not consistent. Increased potassium supply reduced the soluble calcium concentration of young and old laminae. The application of calcium carbonate or phosphate produced an overall increase in the soluble calcium concentration of young and old laminae.

v. Soluble iron. Of the two types of extractant tested, hydrochloric acid saturated with ether appeared to give values better related to the visual appearance of the plants, and more consistent results, than glycerophosphoric acid. In general both reagents extracted more soluble iron from the old laminae of plants supplied with the higher levels of potassium; this response to potassium was sometimes significant when glycerophosphoric acid was used but always so when the other reagent was employed (Table IX).

TABLE IX

Ppm soluble iron, extracted by 0.1 *N* HCl + ether, in the dry matter of laminae. Mean values. August sampling 1949

Treatment level	Young laminae							Old laminae						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
	(± 14.0)			(± 14.0)			(± 8.1)	(± 9.6)			(± 9.6)			(± 5.5)
K_1	27	32	60	42	46	32	40	44	45	47	48	44	44	45
K_2	33	26	44	51	29	23	34	54	59	65	70	74	34	59
K_3	49	50	73	86	61	26	58	74	91	82	109	108	30	82
P_1	33	53	93	—	—	—	60	74	72	82	—	—	—	76
P_2	43	30	63	—	—	—	45	59	82	85	—	—	—	75
P_3	34	25	22	—	—	—	27	40	42	27	—	—	—	36
Mean	37	36	59	—	—	—	44	57	65	65	—	—	—	62
	(± 8.1)							(± 5.5)						

vi. Ash analysis of laminae. Iron concentration (Table X). Addition of iron usually, but not always, produced an overall increase in the iron concentration of both young and old laminae; this increase was largest at the lower P levels. Potassium addition increased the iron concentration of both young and old laminae. The addition of calcium carbonate reduced the iron concentration of young and old laminae; this depressive effect was usually greater in the old than in the young laminae. Phosphate addition markedly decreased the iron concentration of the old laminae and to a lesser extent, of the young laminae; this effect was usually strongest at the high iron levels.

Potassium concentration (Table X). The trends obtained for the total potassium concentration were similar to those obtained for the soluble potassium. Thus iron addition decreased the potassium concentration at the K_1 level and increased it at the K_3 level for the young laminae and increased it at all K levels in the old laminae.

TABLE X

Ppm iron and % potassium in dry matter of laminae. Mean values.
1949 experiment

Treatment level	Iron, ppm							Potassium, %						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
	Young laminae (July)							Young laminae (July)						
	(± 28.2)			(± 28.2)			(± 16.3)	(± 0.19)			(± 0.19)			(± 0.11)
K_1	153	199	177	222	170	138	176	2.6	2.2	1.9	1.6	2.1	2.3	2.0
K_2	174	211	158	200	177	165	181	2.3	2.4	2.1	2.0	2.3	2.5	2.3
K_3	192	225	214	237	210	184	210	3.0	3.9	4.3	3.7	3.9	3.6	3.7
P_1	163	224	272	—	—	—	220	2.4	2.6	2.4	—	—	—	2.4
P_2	205	200	151	—	—	—	185	2.8	2.7	2.7	—	—	—	2.8
P_3	150	210	126	—	—	—	162	2.7	3.2	2.5	—	—	—	2.8
Mean	173	212	183	—	—	—	189	2.6	2.8	2.5	—	—	—	2.7
	(± 16.3)							(± 0.11)						
	Old laminae (August)							Old laminae (July)						
	(± 112)			(± 112)			(± 64.4)	(± 0.10)			(± 0.10)			(± 0.06)
K_1	332	258	529	703	296	119	373	0.4	0.8	0.7	0.7	0.5	0.7	0.6
K_2	343	493	624	719	587	153	486	1.1	1.4	1.7	1.9	1.2	1.2	1.4
K_3	438	640	648	985	572	168	575	4.4	4.9	5.4	5.7	4.8	4.3	4.9
P_1	717	770	920	—	—	—	802	2.4	2.6	3.2	—	—	—	2.8
P_2	265	480	710	—	—	—	485	1.7	2.3	2.6	—	—	—	2.2
P_3	130	140	170	—	—	—	147	1.8	2.3	2.0	—	—	—	2.0
Mean	371	464	600	—	—	—	478	2.0	2.4	2.6	—	—	—	2.3
	(± 64.4)							(± 0.06)						

Increased supplies of potassium were more effective in increasing the potassium concentration of the laminae in the C_2 than in the C_1 plants. The addition of phosphate had no consistent effect on the young laminae but decreased the potassium concentration of the old-especially at the Fe_3 and K_3 levels (Table X).

Phosphorus concentration (Table XI). Increased supplies of either iron or potassium or the addition of calcium carbonate decreased the phosphorus concentration of both young and old laminae.

Calcium concentration (Table XI). Iron addition decreased the calcium concentration of the old laminae; its effect on the young laminae was not consistent. Increased potassium supply usually produced an overall non-linear decrease in the calcium concentration of young and old laminae. Calcium carbonate addition increased the calcium concentration of young and old laminae particularly those of the low iron plants. Increased phosphate supply resulted in an overall increase in the calcium concentration of the old laminae.

vii. Ash analysis of tubers. The addition of iron increased and that of calcium carbonate decreased the iron concentration of the tubers (Table XII). The application of potassium

TABLE XI

% Phosphorus and % calcium in dry matter of laminae. Mean values for July sampling 1949

Treatment level	Phosphorus, %							Calcium, %						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
	Young laminae							Young laminae						
	(± .021)			(± .021)			(± .012)	(± 0.07)			(± 0.07)			(± 0.04)
K_1	.66	.50	.45	.30	.49	.83	.54	1.4	1.2	1.6	1.4	1.3	1.5	1.4
K_2	.54	.45	.41	.27	.42	.72	.47	1.2	1.1	1.2	1.3	1.0	1.1	1.2
K_3	.47	.37	.35	.24	.47	.58	.40	0.6	0.6	0.8	0.6	0.7	0.7	0.7
P_1	.32	.25	.24	—	—	—	.27	1.0	1.0	1.4	—	—	—	1.1
P_2	.52	.44	.32	—	—	—	.42	1.1	0.8	1.0	—	—	—	1.0
P_3	.83	.63	.66	—	—	—	.71	1.1	1.0	1.2	—	—	—	1.1
Mean	.56	.44	.40	—	—	—	.47	1.1	0.9	1.2	—	—	—	1.1
	(± .012)							(± 0.04)						
	Old laminae							Old laminae						
	(± .019)			(± .019)			(± .011)	(± 0.10)			(± 0.10)			(± 0.06)
K_1	.50	.52	.32	.15	.29	.90	.45	3.6	2.9	2.9	3.0	3.5	2.9	3.1
K_2	.47	.38	.31	.13	.22	.80	.38	4.2	3.5	3.2	2.9	4.1	3.8	3.6
K_3	.29	.26	.24	.13	.19	.48	.26	2.3	1.9	1.8	1.7	2.2	2.2	2.0
P_1	.16	.15	.09	—	—	—	.14	3.1	2.2	2.3	—	—	—	2.6
P_2	.27	.26	.18	—	—	—	.23	3.7	3.3	2.7	—	—	—	3.2
P_3	.83	.75	.61	—	—	—	.73	3.3	2.8	2.9	—	—	—	3.0
Mean	.42	.38	.29	—	—	—	.37	3.4	2.8	2.6	—	—	—	2.9
	(± .011)							(± 0.06)						

TABLE XII

Ppm iron (total concentration) in dry matter of tubers. Mean values. 1948 experiment

Treatment level	Fe_1	Fe_2	Fe_3	Fe_4	C_1	C_2	Mean
K_1	10.5	8.6	16.3	23.5	17.1	12.4	14.7
K_2	8.1	9.6	13.6	21.4	14.7	11.7	13.2
	(± 2.21)				(± 1.56)		(± 1.11)
K_3	10.4	8.2	21.3	28.0	20.5	13.3	16.9
K_4	8.3	10.4	21.9	32.4	19.4	17.1	18.2
C_1	9.9	11.1	22.1	28.6	—	—	17.9
	(± 1.56)						(± 0.78)
C_2	8.7	7.3	14.4	24.0	—	—	13.6
Mean	9.3	9.2	18.3	26.3	17.9	13.6	15.8
	(± 1.11)				(± 0.78)		

TABLE XIII

Total iron, potassium and phosphorus concentrations of roots. Mean values for 1949 experiment

Treatment level	Ppm Fe in dry matter						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
		(± 36.2)			(± 36.2)		(± 20.9)
K_1	97	139	517	371	258	125	251
K_2	140	129	685	514	250	172	312
K_3	94	188	941	490	397	337	408
P_1	152	189	1033	—	—	—	458
P_2	101	157	647	—	—	—	302
P_3	78	109	446	—	—	—	211
Mean	111	152	709	—	—	—	324
		(± 20.9)					

Treatment level	% K in dry matter						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
		(± 0.146)			(± 0.146)		(± 0.084)
K_1	0.56	0.40	0.29	0.27	0.36	0.63	0.42
K_2	0.59	0.60	0.55	0.66	0.43	0.64	0.58
K_3	2.46	3.37	1.74	2.50	2.05	3.01	2.52
P_1	1.29	1.35	0.80	—	—	—	1.15
P_2	1.23	1.11	0.48	—	—	—	0.94
P_3	1.08	1.90	1.30	—	—	—	1.43
Mean	1.20	1.45	0.86	—	—	—	3.52
		(± 0.084)					

Treatment level	% P in dry matter						
	Fe_1	Fe_2	Fe_3	P_1	P_2	P_3	Mean
		(± .042)			(± .042)		(± .024)
K_1	.51	.45	.20	.10	.19	.87	.39
K_2	.32	.38	.20	.09	.14	.66	.30
K_3	.37	.27	.16	.08	.11	.62	.27
P_1	.09	.09	.09	—	—	—	.09
P_2	.18	.13	.13	—	—	—	.15
P_3	.93	.89	.33	—	—	—	.72
Mean	.40	.37	.18	—	—	—	.32
		(± .024)					

increased the iron concentration of the tubers at the high iron levels. Generally the variations in iron concentration according to treatment were more consistent in the tubers than in the laminae.

Although not presented here, it was found that the application of iron decreased the potassium concentration at all potassium levels while calcium carbonate usually increased it; the addition of iron or potassium decreased botht he calcium and phosphorus concentrations found in the tubers.

viii. Ash analysis of roots (Table XIII). The nutrient concentrations within the roots were more susceptible to the effect of treatment than were either the laminae or the tubers.

The iron concentration of the roots increased with iron and potassium levels but decreased with phosphate addition.

Increased iron supply linearly decreased the potassium concentration of the roots in the K_1 treatments and gave a non-linear decrease in the K_3 treatments. Phosphate addition decreased the potassium concentration at the Fe_1 level but increased it at higher iron levels.

Increased iron or potassium supplies gave an overall decrease in the phosphorus concentration of the roots. Iron application had no effect on phosphorus concentration at the P_1 level but caused a large decrease at the P_3 level.

5. *Total nutrient content of the potato plant* (1950 experiment)

The results described in this section and sections 6 and 7 refer specifically to the 1950 experiment and deal only with iron, potassium and phosphorus. Although similar data were obtained for calcium and are available for consultation at Long Ashton Research Station, they have been omitted from this paper mainly on the grounds of space and because they do not affect the main conclusions drawn.

The results given in Table XIV were obtained from Blocks 7 and 8

TABLE XIV

Iron content of complete plants and of shoots and tubers; potassium and phosphorus contents of complete plants (Fe expressed as μg; K and P as mg; per 4 plants). Mean values. Blocks 7 and 8. 1950 experiment

	Standard error	Treatment level											
		Fe_1		Fe_3		K_1		K_3		P_1		P_3	
		K_1	K_3	K_1	K_3	P_1	P_3	P_1	P_3	Fe_1	Fe_3	Fe_1	Fe_3
μg Fe/	± 748	4850	6886	7406	8589	5005	7252	7329	8146	5602	6732	6134	9264
complete plants	± 529	5868		7998		6128		7738		6167		7699	
μg Fe/	± 337	4142	5575	4896	6198	4240	4798	5209	6564	5042	4406	4674	6688
shoots and tubers	± 238	4858		5547		4519		5886		4724		5681	
mg K/	± 151	1223	5436	1117	4940	1018	1322	4530	5846	3098	2450	3562	3606
complete plants	± 107	3330		3028		1170		5188		2774		3584	
mg P/	± 9.9	377	395	286	328	128	536	136	586	156	108	616	506
complete plants	± 7.0	386		307		332		361		132		561	

which were chosen for illustration as the effect of treatment on yield, although apparent, was not so marked as in Blocks 3 and 4 (Table IV). Consequently any differences in the nutrient content of the plants grown under different treatments were more likely to be attributed to the direct effect of treatment on uptake and accumulation of the nutrient than to a growth effect.

The iron content of the complete plant increased with iron supply particularly at the K_1 and P_3 levels and with potassium supply at the Fe_1 and P_1 levels (Table XIV). If the total iron content of the shoot and tubers only was considered, and the roots excluded, the standard errors obtained were appreciably smaller and the effect of potassium on iron content became more obvious and was significant at the 1.0% level (Table XIV). The addition of iron decreased the iron content of the shoot plus tubers at the P_1 level but increased it at the P_3 level.

The potassium content of the complete plant increased with increased potassium or phosphate supply (Table XIV), iron addition had little effect.

Increased phosphate supply or of potassium, at the Fe_3 and P_3 levels, increased while iron decreased the phosphorus content of the complete plant (Table XIV).

6. *The relative distribution of nutrients within the potato plant* (1950 experiment)

i. Iron (Fig. 2). Increased iron level increased the proportion of iron found in the roots and tubers. In June (Blocks 7 and 8) added iron generally increased the proportion found in the stems and petioles of the bottom region.

Potassium addition increased, at the June sampling, the proportion of iron found in the stems and petioles of the top region and also in July in the Fe_1P_3 and Fe_3P_1 treatments. Added potassium decreased, in July, the proportion of iron in the lower stems and petioles at the Fe_3P_3 level; this was probably due to tuber formation. Potassium addition markedly increased the proportion of iron found in the tubers and consistently decreased the iron distributed to the roots, at the July sampling. In June there was evidence that at the P_1 level potassium increased the iron found in the roots.

In July, increased phosphate generally decreased the proportion of iron in the roots, except at the Fe_1K_1 level, when it increased.

Phosphate addition usually decreased the proportion of iron found in the tubers except at the Fe_3K_3 level when an increase was

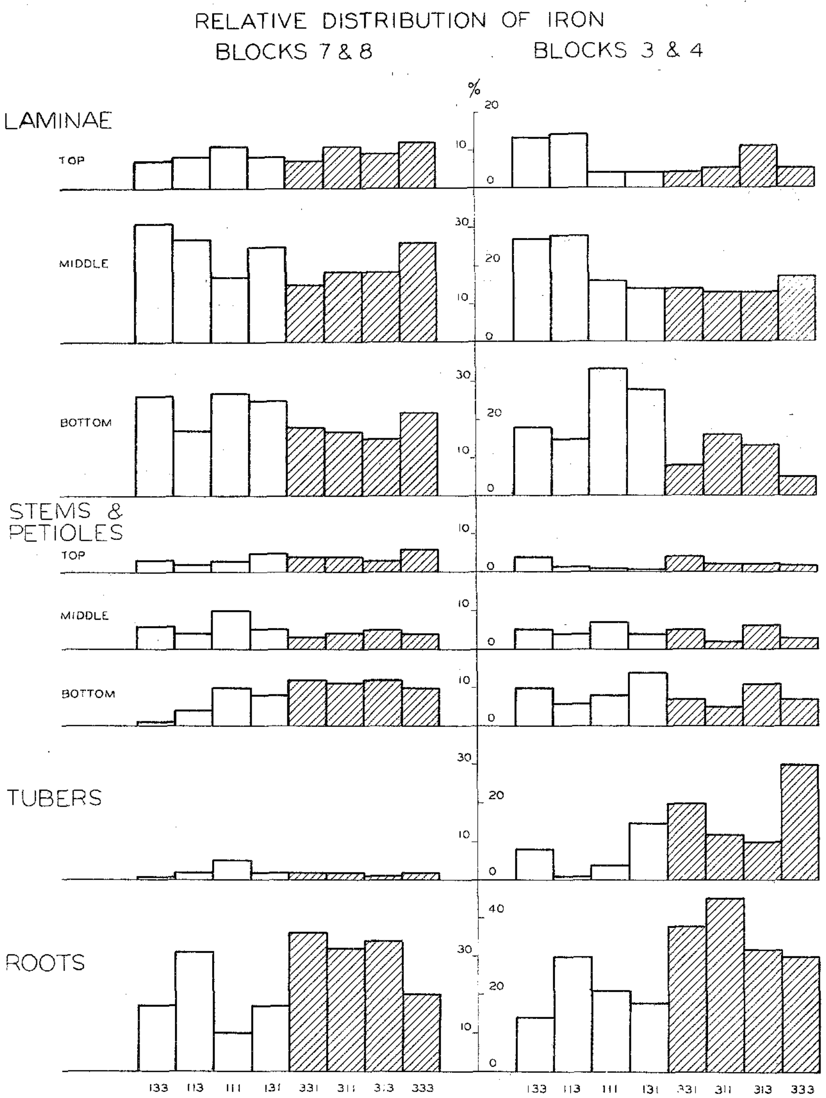

Fig. 2. The relative distribution of iron within the potato plant 40 days (Blocks 7 and 8) and 72 days (Blocks 3 and 4) after planting. The respective levels of Fe, K and P applied are indicated below the lowest histogram; *e.g.* 133 refers to treatment $Fe_1K_3P_3$. 1950 experiment.

obtained. Phosphate had no consistent effect on the proportion of iron in the laminae in June but tended to give an overall increase in July, especially in the upper laminae.

ii. Potassium (Fig. 3). Increased iron supply increased the

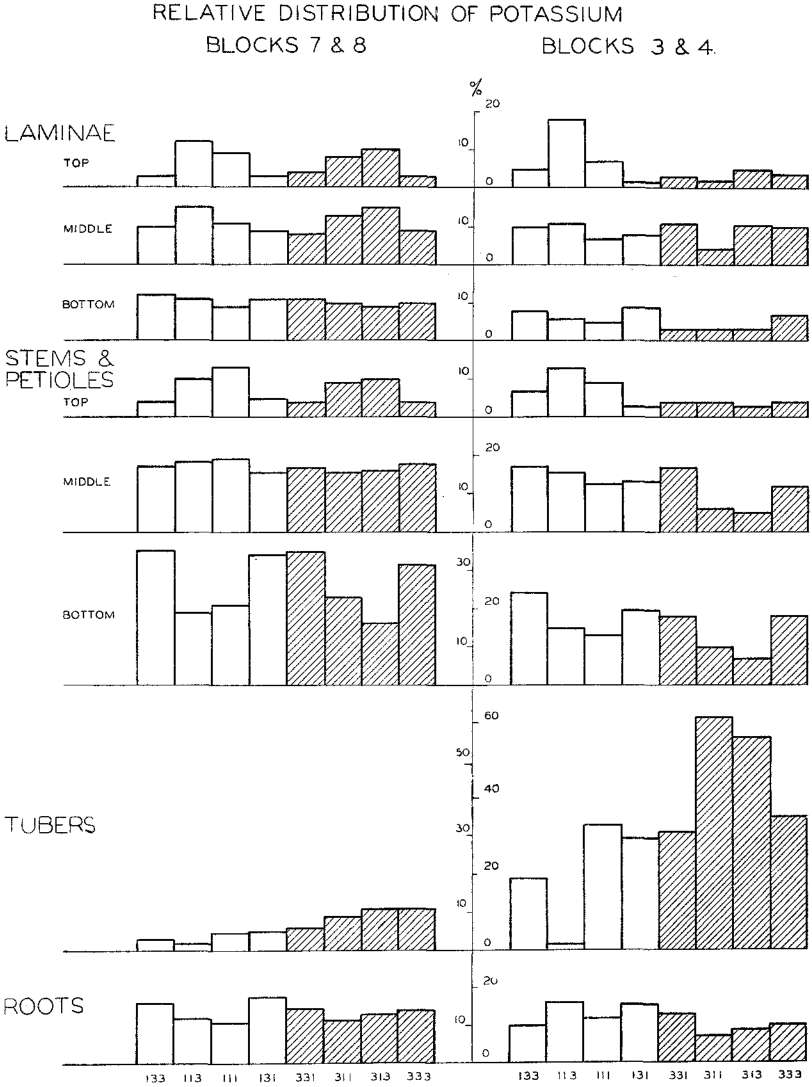

Fig. 3. The relative distribution of potassium within the potato plant. 1950 experiment.

proportion of potassium found in the tubers but usually decreased it, for July, in the roots and top and bottom laminae. A general decrease in the proportion of potassium in the stems and petioles at all levels except the K_3P_1 was obtained on the addition of iron.

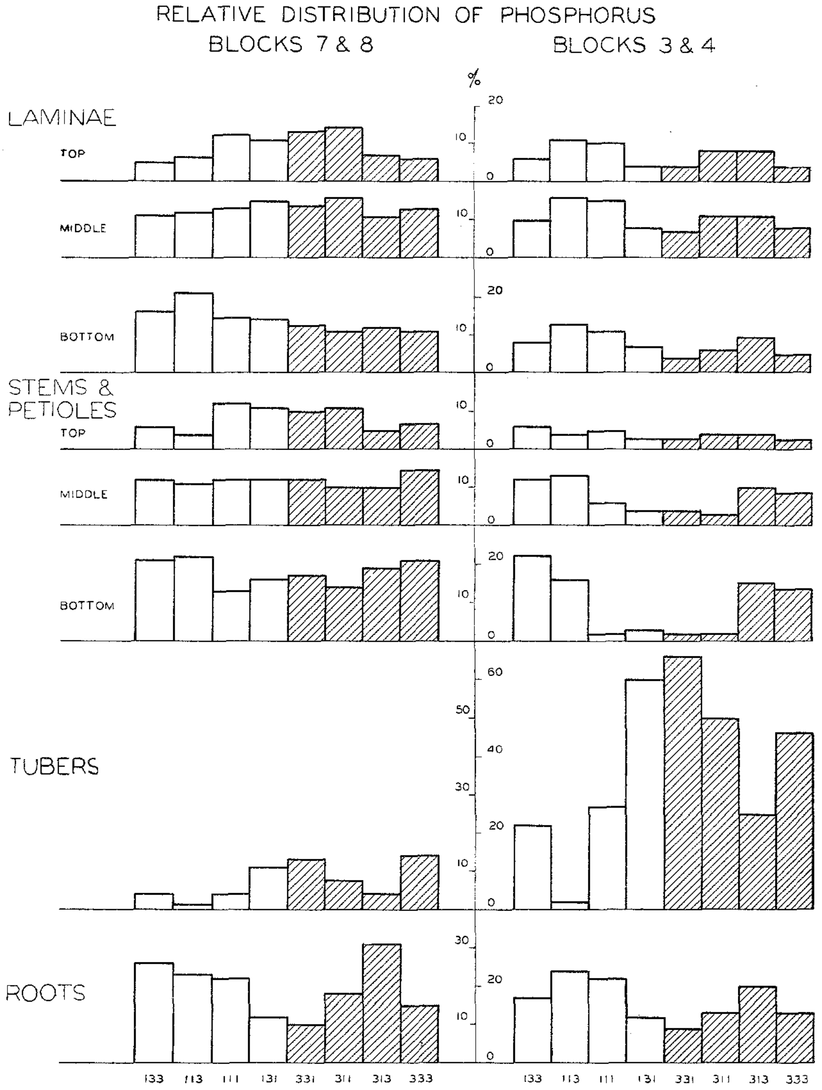

Fig. 4. The relative distribution of phosphorus within the potato plant. 1950 experiment.

Increased potassium supply increased the proportion of potassium found in the roots but decreased it in the tubers, except at the Fe_1P_3 level. Potassium addition decreased the proportion of potassium found in the upper laminae and increased the proportion of potassium in the stems and petioles of the lower regions.

In July increased phosphate supply decreased, (except at the Fe_3K_3 level), the proportion of potassium found in the tubers.

iii. Phosphorus (Fig. 4). The addition of iron generally decreased the proportion of phosphorus found in the roots but increased it in the tubers. Iron addition also decreased the phosphorus content of the laminae and stems and petioles in July.

The addition of potassium usually decreased the phosphorus in the roots but increased it in the tubers. Increased potassium

TABLE XV

Amounts of iron, potassium and phosphorus supplied to potato plants from seed tubers and added nutrients and the percentage of this gross supply absorbed by the plants. Fe, K, and P expressed as mg per 4 plants. 1950 experiment

Treatment	Block number	Amounts supplied from						(C) Total supplied (A) + (B)			% of total (C) taken up by plants		
		(A) Nutrient			(B) Seed tuber *i.e.* content of seed minus mother tubers								
		Fe	K	P	Fe	K	P	Fe	K	P	Fe	K	P
$Fe_1K_1P_1$	3	0.70	1056	422	—1.12	753	50	—0.42	1809	472	—	118	52
	4	0.70	1056	422	—0.42	756	48	+0.28	1812	470	—	95	48
$Fe_1K_3P_1$	3	0.74	17664	442	—2.33	233	42	—1.59	17897	484	—	60	60
	4	0.74	17664	442	—1.17	305	42	—0.43	17969	484	—	60	63
$Fe_1K_1P_3$	3	0.80	1152	4147	+0.41	990	38	+1.21	2142	4185	—	92	32
	4	0.80	1152	4147	+0.12	1198	55	+0.92	2350	4202	—	68	27
$Fe_1K_3P_3$	3	0.78	19200	4320	—0.82	50	—53	—0.04	19250	4267	—	75	34
	4	0.78	19200	4320	—0.97	253	—57	—0.19	19453	4263	—	72	37
$Fe_3K_1P_1$	3	781.2	1008	403	—1.48	705	51	780	1713	454	30	88	37
	4	781.2	1008	403	—1.85	588	47	779	1596	450	27	93	38
$Fe_3K_3P_1$	3	781.2	16128	403	—1.90	285	46	779	16413	449	25	48	44
	4	781.2	16128	403	—2.05	130	44	779	16258	447	23	40	37
$Fe_3K_1P_3$	3	855.6	1104	3974	—0.63	732	18	855	1836	3992	18	104	22
	4	855.6	1104	3974	+0.26	868	1	856	1972	3975	17	86	23
$Fe_3K_3P_3$	3	892.8	18432	4147	—2.10	182	—32	891	18614	4115	41	77	42
	4	892.8	18432	4147	—1.41	467	—36	891	18799	4111	43	64	32

Note: The percentage of iron absorbed from nutrients and seed tubers by the Fe_1 plants cannot be calculated from the data available as the plants obviously obtained large amounts of iron from other sources.

decreased the proportion of phosphorus found in the laminae; this effect was well marked in the top region.

Increased phosphate supply increased the proportion of phosphorus found in the roots but decreased it in the tubers. It also markedly increased the phosphorus found in the stems and petioles of the lower regions for the July sampling. Phosphate addition caused a decrease in the proportion of phosphorus in the upper laminae of the June sampling; in the bottom laminae of both June and July samplings the reverse effect was apparent.

7. *Nutrient absorption as affected by treatment* (1950 experiment)

The amounts of iron, potassium and phosphorus supplied to the plant by the seed tuber and by the application of nutrients, are given in Table XV. These results have been calculated from the volume of nutrients applied to the plants before sampling and from the weight and composition of the seed and mother tubers.

i. Changes in the seed tubers (Table XV). The mother tuber contained more iron at the end of the experiment than was initially present in the seed tuber, except for the $Fe_1K_1P_3$ plants which had depleted the iron content of the seed tubers. This increase in the iron content of the tuber was greater in the K_3 treatments which suggested that increased potassium supply caused iron to return from the plant to the mother tuber.

Plants grown at the K_1 and P_1 levels took up more potassium and phosphorus respectively from the seed tubers than those at the K_3 and P_3 levels. A larger withdrawal of potassium took place at the K_1P_3 than at the K_1P_1 level.

The withdrawal of phosphorus from the seed tuber was greater in the K_1 than in the K_3 treatments. The phosphorus content of the mother tuber in the K_3P_3 treatments was greater than the seed tuber. These results suggested that increased potassium supply caused phosphorus to return from the plant to the tuber.

ii. Percentage uptake of total nutrient supplied (Table XV). The percentage of the total iron supplied, from the nutrients and seed tuber, taken up by the plant – *i.e.* the" percentage uptake" – increased with potassium at the Fe_3P_3 level but decreased slightly at the Fe_3P_1. Unfortunately similar data were not available for the Fe_1 treatments as the plants contained more iron than was supplied to them in solution and from the seed tubers.

This implied that the plants took up large quantities of iron from the sand or from some other source.

The "percentage uptake" of potassium decreased with potassium level but increased with phosphate at the K_3 level. The addition of iron decreased the "percentage uptake" of potassium at the P_1 level but had little effect at the P_3 level.

The "percentage uptake" of phosphorus decreased with phosphate level and also with iron, except at the K_3P_3 level when it increased. Increased potassium supply increased the "percentage uptake" of phosphorus.

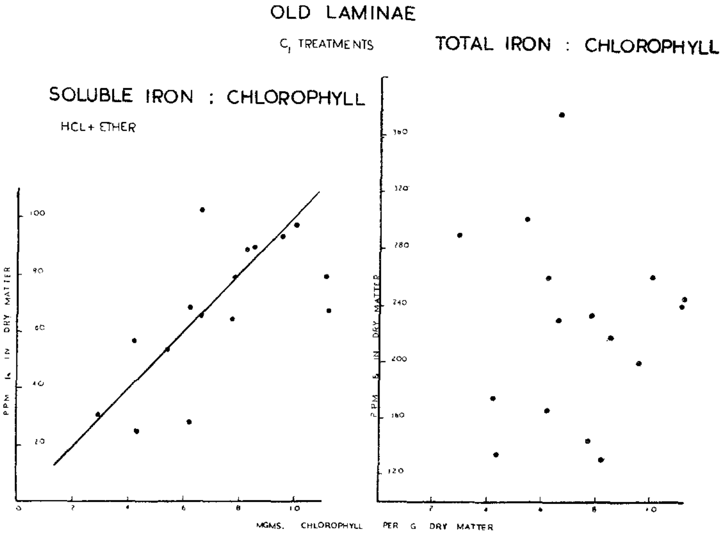

Fig. 5. A comparison of the relationship between (*a*) iron extracted with 0.1 *N* hydrochloric acid saturated with ether, and chlorophyll; (*b*) total iron concentration and chlorophyll. Means of July and August, 1948, values.

THE INTERRELATIONSHIPS OF CHLOROPHYLL, SOLUBLE AND TOTAL NUTRIENTS

1. *Soluble iron in relation to chlorophyll and potassium concentrations*

Both reagents (hydrochloric acid saturated with ether and glycerophosphoric acid) gave soluble iron values for the old laminae which increased with the chlorophyll concentration. In general, for the old laminae these soluble iron values correlated better with the chlorophyll concentration than did the total iron values (Fig. 5).

The curve which related both variables was not always linear in the 1949 experiment as the soluble iron concentration continued to increase when the chlorophyll had ceased to do so. The glycerophosphoric acid values showed a similar correlationship to the chlorophyll concentration of the young laminae whereas the hydrochloric acid values did not. Thus the results suggested that both reagents gave a suitable index for the "available" or "active" iron concentration of the old laminae but that the glycerophosphoric acid values only showed promise for the younger laminae.

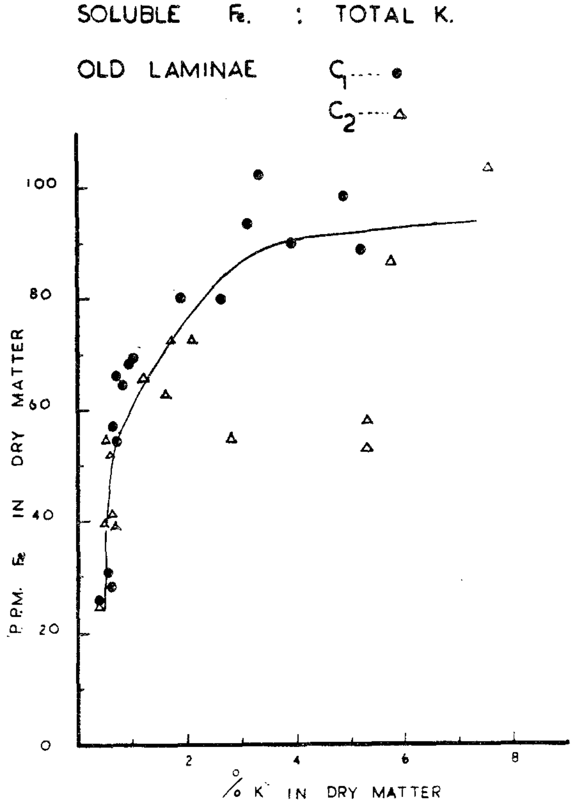

Fig. 6. The variation of iron extracted by 0.1 *N* hydrochloric acid saturated with ether from old laminae, with total potassium concentration. Means of July and August, 1948, values.

The iron extracted from the old laminae with hydrochloric acid saturated with ether increased sharply with the total potassium concentration up to the 1% value and more gradually beyond hist (Fig. 6), the effect was clearer for the C_1 plants. A similar but usually less precise relationship was obtained with the glycerophosphoric acid values for the old laminae.

2. *Young to old lamina ratios for some nutrient elements*

The young/old total potassium ratios decreased sharply at the lower potassium levels with iron application; an overall but less marked decline was also obtained at the higher potassium levels (Fig. 7). Increase in the potassium level consistently decreased the young/old potassium ratio.

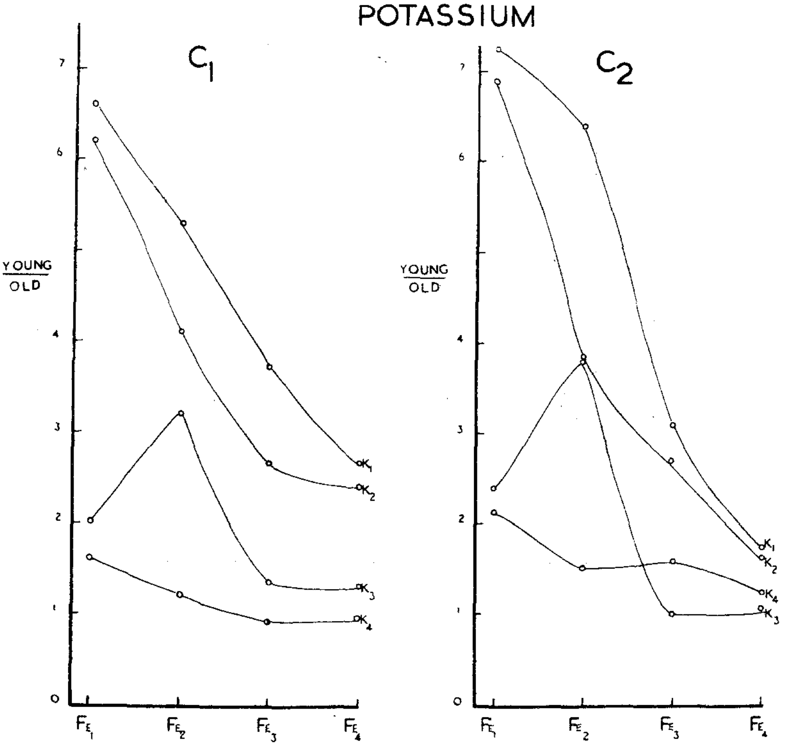

Fig. 7. The variation with iron level of young/old lamina ratios for total potassium concentration. Plotted means of July, August and September, 1948, values. Note sharp decrease in ratio at K_1 and K_2 levels.

3. *Soluble to total ratios for some nutrient elements*

Only a part of the potassium present in the laminae was extracted by Morgan's reagent. The values of soluble/total, potassium ratios, varied between 0.4 and 1.0. This finding supported observations made by Olsen [16]) who concluded that about 30% of the total potassium content in beech leaf cells was adsorptively bound, presumably on the cell proteins. These findings are contrary to the generally accepted view that all the potassium in the cell is readily extractible. The Morgan's-soluble/total potassium ratio tended to increase with potassium and to decrease with iron. The physiological significance of this ratio is not clear but it may well be of some importance in chlorotic foliage.

The ratio of Morgan's-soluble to total phosphorus concentration usually decreased on the addition of potassium and increased with phosphate level.The ratio of soluble/total, phosphorus, appeared in the 1949 experiment, to decrease as the chlorophyll concentration of the old laminae increased. It was this latter relationship, which, although not well defined, prompted the subsequent investigation of inorganic and organic phosphorus fractions in the leaf as affected by varied levels of iron, potassium and phosphate supply (see "4. *Chemical data* iii.").

4. *The interrelationships of chlorophyll, iron and potassium*

The ratio of total iron to total potassium concentration increased in the young laminae and decreased in the old, with increased chlorophyll concentration. This overall relationship, illustrated in Fig. 8, was obtained by plotting values regardless of treatment levels. If as in Fig. 9, the effects of levels are discriminated it is seen that for the young laminae at the lowest potassium level relatively great increases in the Fe/K ratio values were needed to influence the chlorophyll concentration. At high potassium levels the effect of extra iron was diminished and chlorophyll formation was less dependent on the ratio.

The differential response of chlorophyll concentration to varying ratio values according to the age of the laminae reflects the importance of selective sampling in investigations such as this.

5. *The interrelationships of chlorophyll, iron and phosphorus*

The ratio of chlorophyll/total Fe usually decreased as the total phosphorus concentration of the young laminae increased (Fig. 10); the old laminae also revealed this effect in the 1949 but not in the 1948 experiment.

The chlorophyll content of young and old laminae increased sharply with increase of the ratio of total iron to phosphorus at the

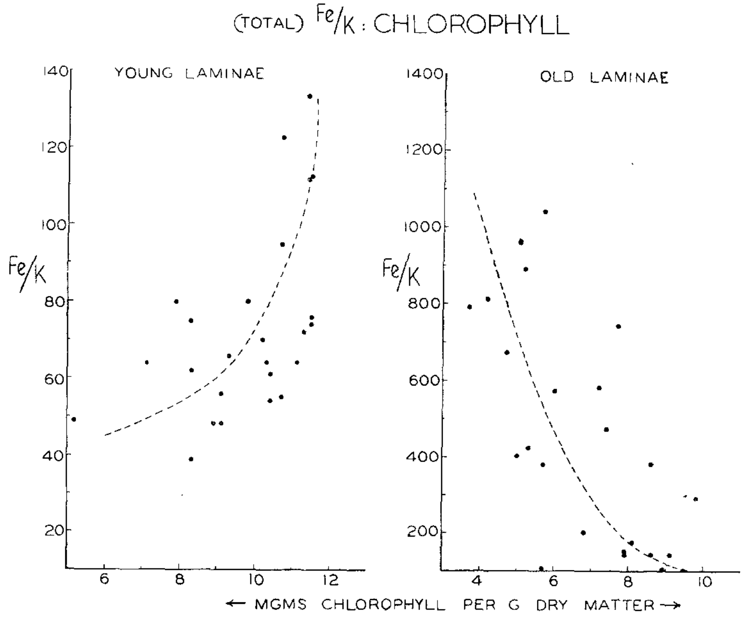

Fig. 8. The variation of the total Fe/total K ratio with the chlorophyll concentration of young and old laminae. July, 1949, sampling.

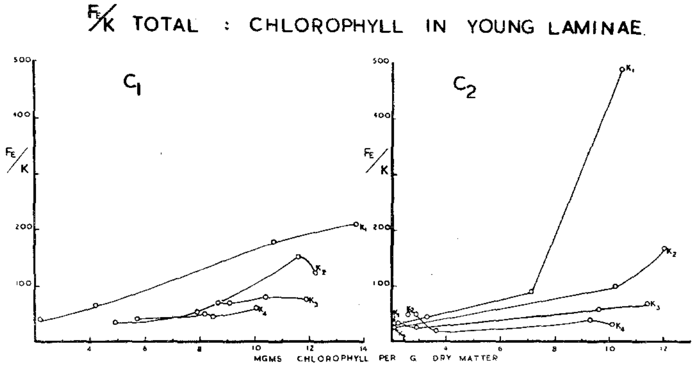

Fig. 9. The variation of the total Fe/total K ratio with chlorophyll concentration of young laminae. Plotted means of July, August and September, 1948, values.

Fe_1 level; the same effect was also obvious at the Fe_1 and Fe_2 levels in the old laminae (Fig. 11). At the Fe_2 and Fe_3 levels in the young and at the Fe_3 level in the old laminae large increases in the ratio decreased the chlorophyll concentration.

6. *The interrelationships of chlorophyll, potassium and phosphorus*

The relationship between the total K/P ratio and chlorophyll concentration was clearly governed by the iron status and was also probably related to the secondary calcium deficiency effects.

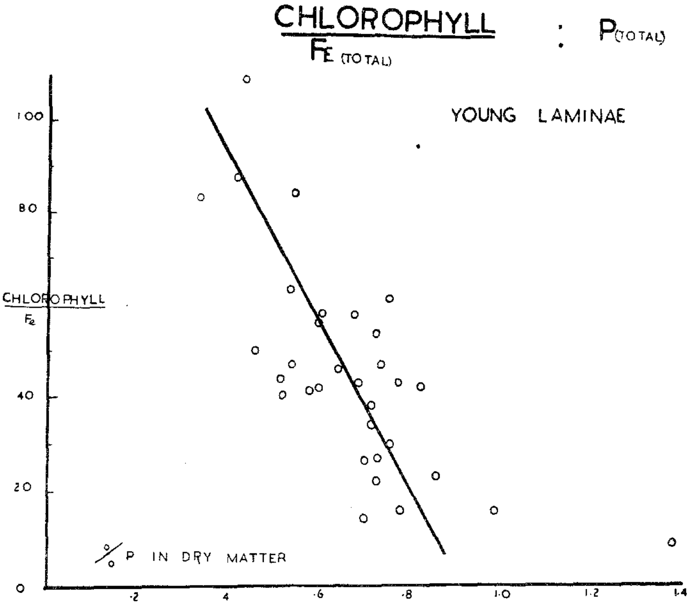

Fig. 10. The variation of the ratio of chlorophyll/total Fe with the total phosphorus concentration of the young laminae. Plotted means of July and August, 1948, values.

Thus the chlorophyll concentration increased as the K/P ratio increased in the young laminae at the Fe_1 level and in the old laminae at the Fe_1 and Fe_2 levels (Fig. 12). A decrease in chlorophyll with increase in the total K/P ratio occurred at the Fe_2 and Fe_3 levels in the young and at the Fe_3 level in the old laminae. The chlorophyll increase with K/P ratio was sharpest at the Fe_1 level in the young but grew steeper with increased Fe level in the old laminae (Fig. 12).

7. *The interrelationships of chlorophyll, calcium and potassium*

The chlorophyll concentration of the young laminae of the K_1 and

K_2 treatments increased as the total Ca/total K ratio increased; this effect was much more striking in the C_2 than in the C_1 treatments (Fig. 13). Slight increases were also obtained in the K_3 treatments but at the K_4 level chlorophyll concentration was not correlated with the Ca/K ratio. These statements describe the effects observed in the 1948 experiment but identical relationships were obtained in subsequent experiments which revealed that the Ca/K ratio only varied with chlorophyll concentration at the deficiency level of potassium, and showed that the relationship was independent of the presence of added calcium carbonate.

In all experiments the chlorophyll concentration of the old laminae showed an overall decrease with increased Ca/K ratio value.

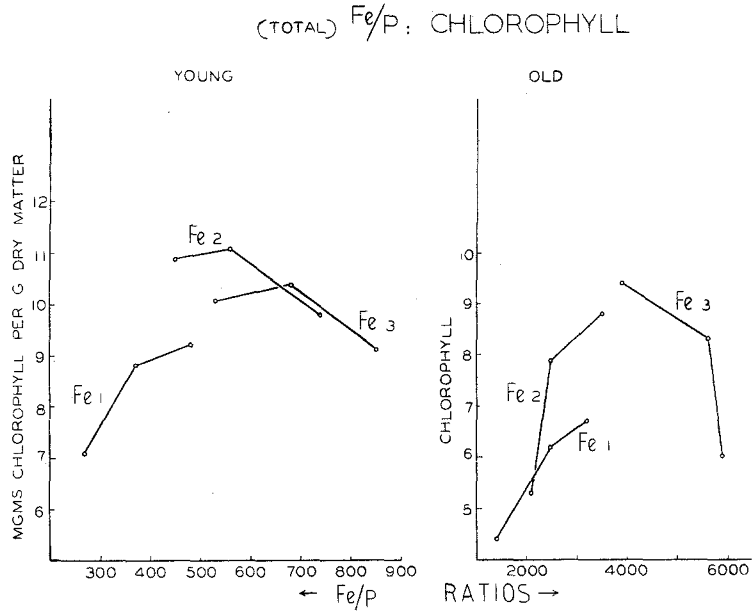

Fig. 11. The relationship between the total Fe/total P ratio and the chlorophyll concentration of young and old laminae. Mean values for July, 1949, sampling. Note similarity between Fe_1 — young and Fe_1 and Fe_2 — old.

DISCUSSION

Many of the visual effects previously described [9]) have now been shown to occur in the potato in the presence of calcium carbonate or high levels of phosphate; in particular the "Fe/K visual response"

(Plate II) and the delaying effect of iron on the inception of potassium deficiency (Plate IV). The response to potassium at deficiency levels of iron could not be attributed to any iron accidentally supplied by the extra potassium salts as analysis of the nutrients did not reveal any such contamination. Neither could the response be attributed to the high sulphate concentration of the higher potassium nutrients; an experiment carried out in 1951, to test this point, showed that at a low level of potassium supply, increased sulphate concentration did not prevent the appearance of chlorosis in the Fe_1P_3 plants. The delaying effect of iron on the inception of potassium deficiency was consistent with the pronounced effect of iron supply on the relative concentrations of potassium found in the young and old laminae (Fig. 7); this reduced young/old, potassium ratio, probably reflected the effect of iron on the translocation and distribution of potassium within the plant.

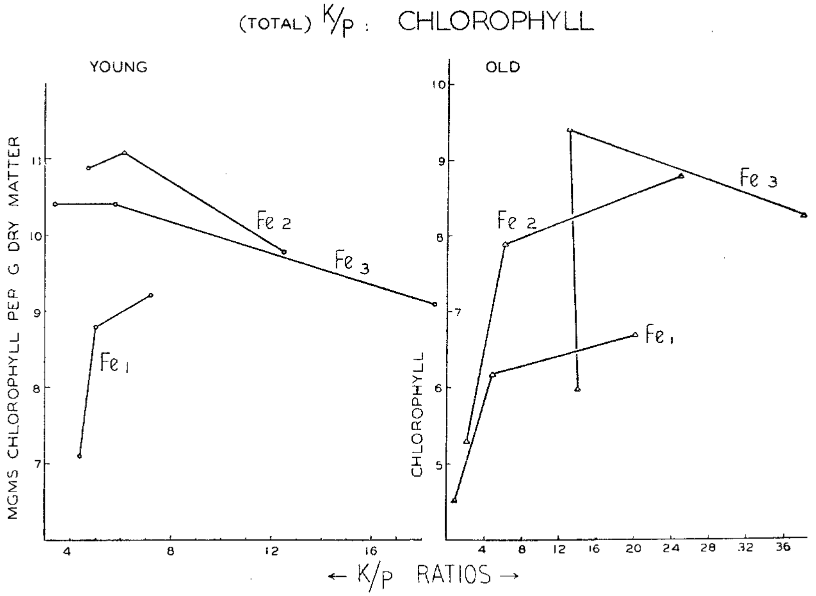

Fig. 12. The variation of the total K/total P ratio with the chlorophyll concentration of young and old laminae. Mean values for July, 1949, sampling.

The addition of calcium carbonate increased the pH of the sand and decreased the concentration of iron in the laminae. Calcium carbonate did not however, cause any fundamental change in the symptoms or relationships observed but merely modified the relative severity, critical concentration or time of appearance.

The Ca/K ratio of the young laminae increased with chlorophyll concentration when the potassium supply was limited but not at the higher potassium levels (Fig. 13). A low Ca/K ratio did not necessarily imply that the foliage was chlorotic as some of the smallest values obtained were for the higher potassium plants which did not show chlorosis. The relationship between chlorophyll and the Ca/K ratio was emphasised by the addition of calcium carbonate but was also obvious in the C_1 treatments; the relationship was therefore general, as confirmed by the 1949 experiment, and independent of the presence of calcium carbonate. Under field conditions of lime-induced chlorosis where the low Ca/K ratio is generally found, circumstances are also conducive to potassium deficiency and this may be incipient if not visually evident when the Ca/K ratio becomes abnormal. Hence the importance of the Ca/K ratio in

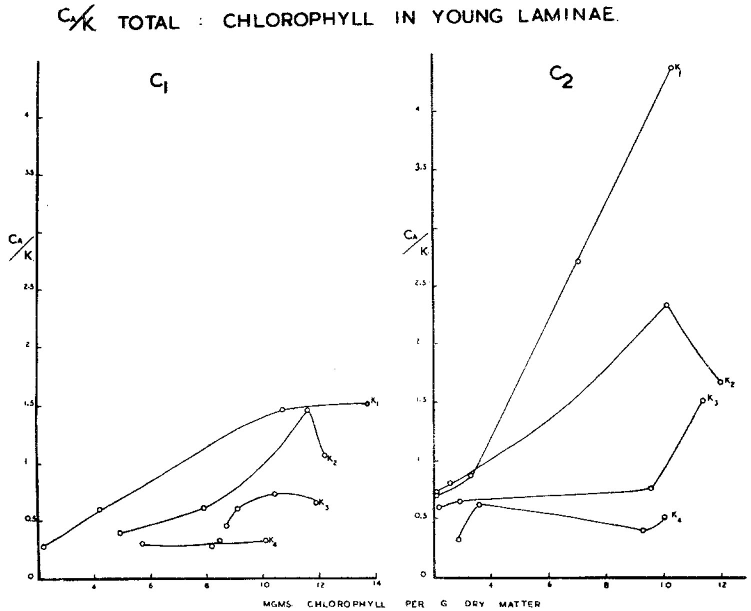

Fig. 13. The variation of the total Ca/total K ratio with chlorophyll concentration of the *young* laminae. Plotted mean of July, August and September, 1948, values.

instances of lime-induced chlorosis in the field was now confirmed. The addition of iron in the nutrient raised the Ca/K ratio when potassium was deficient and thus illustrated the curative effect of iron on lime-induced chlorosis. It is probable that the interrelationship between the Ca/K ratio and chlorophyll concentration of the young laminae reflected the effect of, rather than caused, the different iron status of chlorotic and green plants.

Calcium deficiency symptoms induced by high iron and potassium supplies and associated with a low phosphorus concentration in the laminae (Plate VI) were accompanied by the incidence of medullary necrosis in the tubers (Plate VIII). The medullary necrosis symptoms agreed closely with those described as occurring naturally in the Dutch East Indies by Schwarz [25]) and those produced in culture solutions under conditions of calcium deficiency by Van Schreven [33]). Van der Plank [32]) found similar necrotic symptoms in tubers grown in strongly acid soils but there were no external or foliage symptoms and control was effected by the application of lime and superphosphate at planting time. It appears that the medullary necrosis reported here was due to a deficiency of calcium accentuated by or associated with a high potassium and low phosphorus status (Table II) and which was accompanied by the characteristic symptoms described for the shoot (Plate VII).

Some of the experiments clearly revealed the parallel and similar effects of iron and potassium in certain aspects of plant nutrition and the opposite effects exerted by phosphate. Thus application of either iron or potassium (Plate II) cured iron deficiency chlorosis, induced and increased the severity of phosphorus deficiency symptoms and accentuated the severity of calcium deficiency symptoms (Plate VII). Extra phosphate supply, however, induced and increased the severity of iron deficiency chlorosis (Plates I and III) and of potassium deficiency symptoms, and reduced the severity of the calcium deficiency. In addition to the above visual effects phosphate exerted a reverse effect to iron and/or potassium on dry weight of shoots and roots, incidence of medullary necrosis (Table II), chlorophyll (Table V), phosphorus and calcium (Table XI) soluble and total iron (Tables IX and X) concentrations of the old laminae and total iron concentration of tubers and roots (Tables XII and XIII). Thus, to a large extent iron and potassium exerted similar effects which suggests that both may influence similar physiological behaviour. It is known that deficiencies of either may cause the accumulation of various soluble organic nitrogen fractions 1) 10) 20) 24) 28) 29) 30) 35) and a depletion of polysaccharides 1) 6) 15) 22) 26) 27). Both may influence various respiratory systems but there is no known instance in which both iron and potassium perform the same function.

On the other hand there were other effects which emphasized the reciprocal nature of the relationship between iron and potassium. Thus whereas increased potassium supply increased the iron concentration of the laminae, tubers and roots and decreased the severity of iron deficiency symptoms, increased iron supply decreased the potassium concentration of young laminae (Table X), tubers and roots (Table XIII) at the K_1 level and increased the severity of the potassium deficiency symptoms (Plate V).

Increased phosphate supply decreased the concentration of iron and increased iron supply decreased the concentration of phosphorus found in the roots (Table XIII). Despite the decreased iron concentration in the roots, as a result of phosphate addition, the total amount of iron localised in the roots usually increased as a result of the beneficial effect of phosphorus on root production but increased iron supply not only decreased the concentration of phosphorus in the roots but also the total amount localised in them. There was no evidence to suggest that at the high phosphate levels iron accumulated in or was precipitated as ferric phosphate, within the roots.

The role of potassium in mitigating the chlorosis due to lack of iron may be associated with an increased iron (Tables IX and X) and reduced phosphorus concentration (Table XI) of the laminae; these changes were accompanied in the old laminae by an overall increase in the chlorophyll/Fe ratio and a decrease in the Fe/K ratio (Fig. 8). Thus it appeared that apart from either the possibility of improved absorption of the existing iron supply or a different distribution of iron within the plant the beneficial effect of potassium on chlorosis may have been due to an enhanced efficiency of iron utilisation for chlorophyll formation.

The favourable effect of potassium level on chlorophyll production in the young laminae at low iron levels (Table V) and the decreasing influence of potassium as the iron supply was increased, also suggested that restricted supplies of iron in the nutrient solution were used more efficiently in the presence of adequate potassium.

The steady decrease with extra potassium of the slope which related the Fe/K ratio of the young laminae to the chlorophyll concentration was further evidence (Fig. 9). It implied that at the highest potassium levels only a small increase in the proportion of iron was necessary to give a large increase in chlorophyll *i.e.* the efficiency of the added iron was at its maximum or was no longer limiting. For the young laminae at the Fe_1P_2 and Fe_1P_3 levels large increases in chlorophyll concentration, accompanied by slight increases in iron concentration, were observed on potassium addition thus giving an increased chlorophyll/Fe ratio. When, however, iron was not lacking as at the Fe_1P_1 and the Fe_2 and Fe_3 treatments, potassium addition usually gave a well marked increase in iron concentration and decreased the chlorophyll and phosphorus concentrations of the young laminae; consequently the chlorophyll/Fe ratio decreased.

The young laminae of the Fe_1P_2 and Fe_1P_3 plants responded to potassium application in the same manner as the old laminae; in both the efficiency of iron utilisation was increased and phosphorus concentration decreased.Thus it might be assumed that this increased efficiency of iron was related to a depression of phosphorus concentration. On this basis, the inhibitory influence of potassium on chlorophyll production in the young laminae of the higher iron plants (Table V) may be attributed to the cumulative effect of iron and potassium on the production of calcium deficiency symptoms and a reduced phosphorus status—pathological conditions which hampered chlorophyll production.

Support for the theory that the effect of potassium on increasing the efficiency of iron was due to the reduction in phosphorus was apparent in the increased chlorophyll/Fe ratio obtained with decreased phosphorus concentration (Fig. 10)) and in the increased chlorophyll concentration of the laminae obtained with increase in the Fe/P ratio at deficiency levels of iron (Fig. 11). It was obvious that at the lower iron levels the K/P ratio played an important role in chlorophyll formation (Fig. 12). With both the Fe/P and K/P ratios the young laminae of the Fe_1 plants showed a greater similarity to the old laminae of the Fe_1 and Fe_2 plants than to the Fe_2 and Fe_3 young laminae (Figs. 11, 12).

The 1949 and subsequent experiments showed that when the *overall mean* values for the chlorophyll/Fe ratio were plotted against the corresponding phosphorus concentrations a similar relationship to that depicted for the 1948 experiment (Fig. 18) was obtained. However, scrutiny of the individual results indicated that the chlorophyll/Fe ratio increased with phosphate level when the iron and potassium supplies were *not* limiting growth. Thus an increased phosphorus concentration of the laminae did not *per se* decrease the efficiency of iron utilisation. It appeared that the effect of added potassium in curing chlorosis might be the prevention of iron precipitation by the phosphorus present either by the conversion of the inorganic to organic phosphorus or by some secondary effect on organic acid status and cell sap pH.

If the role of potassium in increasing the efficiency of iron utilisason was partially due to a production of a low tissue pH, the statements of Ingalls and Shive[11]), Rogers and Shive[21]), Schander[23]), Pierre and Bower[18]), and Weiss[39]) suggest that decrease of the pH would be accompanied by an increase in soluble iron. The results, which have been described, showed, in fact, that the soluble iron increased with potassium supply (Table IX).

Fig. 5, clearly confirms the importance of soluble fractions and illustrates the better relationship obtained between soluble iron and chlorophyll than that obtained with total iron. It was also possible to relate the soluble iron extracted by the hydrochloric acid reagent to the potassium concentration of the old laminae (Fig. 6); this fraction may therefore be regarded as a measure of the efficiency of potassium in enhancing the utilisation of iron in chlorophyll production. The poor correspondence between total iron and chlorophyll may have reflected the analytical difficulties of iron determination in dry material due to the presence of silica [12]) or it may imply that the total iron status was not closely related to chlorophyll production. The chlorophyll/soluble or total iron, ratios, decreased markedly with time; this confirmed Bennett's[1]) findings. It suggested that the soluble iron (determined with either glycerophosphoric acid or hydrochloric acid reagent) did not accurately represent the fraction of iron active in chlorophyll formation, or that other factors, later in the season, became limiting.

There is evidence in the literature to suggest that increased potassium supply increased organic acid content [5]) [22]) [34]), while increased phosphate decreased it [37]). Chlorosis may also be accompanied by a change in the organic acid constituents of the leaf [10]) [13]). Thus it was possible that the effect of potassium on soluble iron concentration and on the utilisation of iron might have operated through its effect on organic acid status which in turn would influence tissue pH.

It was actually found (Table VI) that increased potassium supply usually increased the titratable acidity of the old laminae but decreased that of the young. This beneficial effect on the titratable acidity of the old laminae cannot however be the chief role of potassium in increasing the efficiency of iron utilisation as potassium addition depressed the acidity of the green young laminae in plants which showed the "Fe/K visual response".

The suspected presence of an organic acid which increased in the laminae when plants were supplied with extra potassium and which decreased in iron deficient laminae was of great interest and merits further investigation. The increased occurrence of this acid may conceivably have prevented the immobilisation of iron within the lamina. This interpretation also implies that increased potassium status enhanced the synthesis of this acid within the laminae. The feeding of malic, citric or oxalic acids to iron deficient plants did not cure the chlorosis; in fact, oxalic acid markedly accentuated its severity. The acids, if absorbed, were rapidly converted to other compounds and could not be detected in appreciable amounts in the laminae.

It has been suggested above that one of the roles of potassium in increasing chlorophyll production at iron deficiency levels may be to reduce the ability of phosphorus to immobilise the iron in the lamina. It was therefore interesting to note (see INTERRELATIONSHIPS, 3) that the ratio of Morgan's-soluble/total, phosphorus concentration, decreased with increased chlorophyll concentration of the old laminae. It may be inferred that the soluble phosphorus, as determined here, represented the metabolically less active fraction of the total. Further support for this probable role of potassium is given in Table VII. Increased potassium level was found to decrease the concentration of inorganic phosphorus and the ratio of inorganic to organic phosphorus present in the lamina. The preponderance of inorganic phosphorus in iron deficient laminae was therefore probably associated with an inability, due to the lack of potassium, to use the phosphorus in metabolic processes. It may be assumed that a large excess of inorganic phosphorus would effectively immobilise the relatively small amount of iron present in iron deficient laminae. Consequently part of the effect of potassium on iron utilisation appears to be indirect and to be associated with the conversion of inorganic phosphorus to some organic phosphorus-containing compound which is assumed to be less capable of immobilising the iron in an "inactive" or "unavailable" form.

The foregoing discussion, based mainly on the results of the 1948, 1949 and 1951 experiments, shows that the effect of potassium in ameliorating the severity of iron deficiency chlorosis was partially due to a greater concentration of iron in the lamina and partly due to an increased efficiency of iron utilisation for chlorophyll formation. The 1950 experiment provided information as to whether a greater amount of iron was taken into the plant and the distribution of the various nutrient elements under varied conditions; the remaining part of this discussion deals principally with the results of that experiment.

A the Fe_1P_3 level increased potassium supply decreased the proportion of iron found in the roots but increased it in the tubers and also in the stems and petioles (Fig.2). Increased potassium level increased the "percentage uptake" of iron at the Fe_3P_3 level (Table XV). It is assumed that a similar increased efficiency of iron absorption took place at the Fe_1 level. This was supported by the highly significant increase in "absolute" iron content of the shoot and tubers obtained with increased potassium at all iron levels (Table XIV).

Increased potassium supply also increased the iron content of the complete plant. The effect of potassium on total iron content of the complete plant was not as clearly defined as those obtained for the shoot plus tubers (Table XIV). Inspection of the individual data showed, however, that there was only one exception to the positive effect of potassium on total iron content and that the errors in root analysis, due probably to contamination by the sand, were particularly large. Under these circumstances the conclusion that potassium exerted a real effect would seem to be justified.

It was therefore concluded that one effect of potassium was to increase the mobility of iron within the plant and to facilitate its distribution to the more actively growing regions. A second effect might be inferred — namely that potassium increased the efficiency of iron absorption by the plant.

The addition of phosphate at the Fe_1K_1 level decreased the proportion of iron found in the tubers, stems and petioles and in the bottom laminae but increased it in the roots and in the upper laminae (Fig. 2). Increased phosphate supply also increased the "percentage uptake" of iron at the Fe_3K_3 level but decreased it at the Fe_3K_1 level (Table XV). If the same effect applied at the Fe_1 level, it would accord with visual observation and would explain the occurrence of chlorosis on the addition of phosphate at the Fe_1K_1 level and the production of tall vigorous plants at the Fe_1K_3 level.

Hence it was concluded that the effects of phosphate addition at the Fe_1K_1 level were to retain the iron in the roots, owing to increased root production, and possibly to "immobilise" it in the upper laminae, where chlorosis was obvious. It also interfered with iron absorption at low potassium levels.

Increased iron supply decreased slightly the potassium content of the complete plant but this effect was not significant (Table XIV). Added iron, however, markedly influenced the distribution of potassium within the plant. It increased the proportion found in the tubers but decreased it in the laminae and stems and petioles (Fig. 3). This effect became more marked with time, especially at the K_1P_3 level. This altered distribution was consistent with both the greater ultimate severity of the potassium deficiency and larger tuber production at the Fe_3 level.

Increased iron or potassium supply decreased the proportion of phosphorus found in the roots and laminae but increased it in the tubers (Fig. 4). This distribution was apparently conducive to the appearance of phosphorus deficiency symptoms.

The experimental evidence suggested that increased potassium status may cause the migration of iron and phosphorus from the plant to the mother tuber during the growth period (Table XV). The application of phosphate, however, usually caused an increase in the absolute amount of iron withdrawn from the seed tuber. These effects were paralleled by the influence of treatments on the relative distribution of nutrients to the newly formed tubers. Thus the proportion of iron and phosphorus generally increased with iron or potassium application but decreased with phosphate (Figs. 2, 4). The addition of iron increased the proportion of potassium found in the tubers but potassium or phosphate generally decreased it (Fig.3).

It was remarkable that, despite the free drainage of each pot, the efficiency of potassium absorption, as expressed by the "percentage uptake", was 80% or more, in the K_1 treatments. In the $Fe_1K_1P_1$ treatments the absorption was 100% — allowing for experimental error (Table XV). The efficiency of the plants in absorbing phosphorus was much less.

The addition of iron decreased the efficiency of potassium absorption at the P_1 level but increased it at the K_1P_3 level and had no effect at the K_3P_3 level (Table XV). The addition of potassium decreased at the Fe_3P_1 but increased at the Fe_3P_3 level the "percentage uptake" of iron. Hence the effect of iron on the efficiency of potassium absorption and of potassium on the efficiency of iron absorption depended on the phosphate level. The relationship between iron and potassium could not therefore be defined as a simple antagonism or synergism. In a similar manner the effect of phosphate on the "percentage uptake" of iron depended upon the K level.

On the other hand the interrelationship between potassium and phosphorus approximated to that of synergism. Increase of potassium level increased the percentage uptake of phosphorus; phosphate addition increased the uptake of potassium at the K_3 level, but reduced it at the Fe_1K_1 level (Table XV). In spite of the increased efficiency of phosphorus uptake at the Fe_1P_1 level due to potassium, the visual response was one of increased severity of phosphorus deficiency owing to the more widely disturbed nutrient balance in the plant.

The results showed clearly that a discussion of the effect of treatment on the nutrient status of the plant depended greatly upon both the region sampled and the age of the plant. The interaction between iron and potassium and between iron and phosphorus were especially subject to this qualification. In addition there was a modifying effect of the third element on the interaction of the other two.

GENERAL SUMMARY AND CONCLUSIONS

1. Iron and potassium were shown to be interrelated in the metabolism of the potato plant. The nature of this interrelationship was dependent on the level of phosphate supply.

2. When iron supplies were limiting, chlorosis was induced or accentuated by the addition of calcium carbonate, by the addition of phosphate, or by a reduction in the supply of potassium.

3. Iron deficiency chlorosis was cured by the addition of high levels of potassium. This response to potassium was associated with an increased iron concentration in the lamina and with a greater efficiency of iron utilisation in chlorophyll formation.

4. It was suggested that the effect of potassium on the iron content of the lamina was due to an increased mobility of iron in the plant, inferred from a study of nutrient uptake and distribution. This enhanced mobility was associated with a reduction in the proportion of iron localised in the roots in the presence of a plentiful supply of phosphate.

5. The increased efficiency of iron utilisation was attributed both to the depression in the total phosphorus concentration and also to the decrease in the concentration of inorganic phosphorus and in the ratio inorganic/organic phosphorus found in the lamina.

6. The chlorophyll concentration of the young laminae of potassium deficient plants varied with the Ca/K ratio; this relationship was independent of the presence of calcium carbonate and was dependent on the iron status of the plant.

7. Iron status governed the distribution of potassium within the plant; high iron levels favoured its translocation to the tubers at the expense of the young shoot regions and altered the gradient of concentration between young and old laminae.

8. The work as whole illustrated the importance of the age of the tissue and of the selection of the morphological region sampled in assessing nutrient interrelationships, and of the modifying effect of any one nutrient on the precise nature of the interaction between the others studied.

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