# NUTRIENT INTERACTIONS AND DEFICIENCY DIAGNOSIS IN THE LETTUCE

#### IV. PHOSPHORUS CONTENT AND RESPONSE TO PHOSPHORUS

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#### Summary

Lettuce plants grown in sand culture, and receiving nitrogen, phosphorus, and potassium at five levels in all combinations, were analysed at different stages of growth for these elements. An attempt was made to relate these analytical data to the growth response following a supplementary application of phosphorus.

The concentration of phosphorus in the plant dry matter was usually increased by increasing levels of phosphorus supply, decreased by additions of the other nutrients. Increases in phosphorus content were greatest when potassium was deficient or when nitrogen was abundant.

The increase in dry weight of the plants, as a response to additional phosphorus supplied at 46 days from sowing, was closely related to the phosphorus content of the plants previously; there was no clear evidence that this relationship depended on the nitrogen or potassium content of the plants. The date of sampling for analysis (between 29 and 44 days from sowing) did not appear to affect the precision with which response to phosphorus could be forecast. There seemed to be no advantage in analysing selected organs. The relationship between phosphorus content and response was approximately linear.

#### I. INTRODUCTION

As was explained in the first paper of this series (Goodall, Grant Lipp, and Slater 1955), the primary purpose of this experiment was to investigate the forecasting of major element deficiencies by chemical analysis of plant material at an early stage of growth. To this end, plants of widely varying nutritional status were grown in sand culture. Samples of these were harvested at several stages, dry weights obtained, and the nitrogen, phosphorus, and potassium contents determined. Further supplies of nutrients were then added, and the resulting increases in dry weight measured with a view to correlating these responses with the chemical analysis.

Previous papers have dealt with the results in terms of dry weight (Goodall *et al.* 1955), water content (Goodall, Slater, and Grant Lipp 1957) and nitrogen relations (Slater and Goodall 1957). The present paper covers the uptake of phosphorus and its concentration in the plant tissues, and the relation between the

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<sup>†</sup> Botany School, University of Melbourne; present address: Tobacco Research Institute, Mareeba, Qld. responses to additional supplies of this element on the one hand, and the composition of the plants on the other. A subsequent paper will deal similarly with potassium content and responses.

# II. MATERIALS AND METHODS

Details of the design of the experiment, application and composition of nutrients, and harvesting procedure are given in the first paper. Only a brief summary is included here.

The amounts of the nutrients supplied per pot were as follows:

Nutrient level	1	<b>2</b>	3	4	<b>5</b>
N as NaNO <sub>3</sub> (mg)	50	200	500	2000	5000
P as Na <sub>2</sub> HPO <sub>4</sub> (mg)	<b>2</b>	5	20	100	500
K as K <sub>2</sub> SO <sub>4</sub> (mg)	0	100	300	1000	3000

These treatments were applied initially in all combinations, together with an adequate supply of other requisite nutrients. At 46 days after sowing, each of the following subtreatments

$S_N$	200 mg N per pot
$S_P$	20  mg  P per pot
$S_K$	100 mg K per pot

was applied to one of the four pots subjected to each of the 125 initial treatments, the remaining 125 pots being left without subtreatment as controls.

Sample plants were removed for analysis at 11, 22, 29, 37, and 44 days from planting, and the remainder were harvested at 98 days. The analyses at 11 days were performed on the whole plants; on later occasions only the aerial portions were analysed. At 11 and 22 days, the treatments sampled consisted of levels 1, 3, and 5 of each nutrient in all combinations—27 in all. At 29, 37, and 44 days, samples were analysed from all phosphorus levels and levels 1, 2, 3, and 5 of the other nutrients, again in all combinations, making 80 treatments in all. At 44 days, the plants were separated into younger leaves, older leaf laminae, and older midribs, wherever this would yield samples large enough for analysis. At 98 days, the weight of plant material available from each treatment was in many cases very small, and consequently full analytical results could be obtained only for a minority of the treatments.

After dry weight determination the plants were ground and re-dried at 100°C prior to analysis. For the determination of total phosphorus, samples of material weighing approximately 20 mg, and containing  $15-100 \ \mu g$  P were digested with concentrated suphuric acid and 100-volume hydrogen peroxide over a low Bunsen flame. Digests were diluted and aliquots taken for colorimetric determination. These determinations were performed using a modification of Fiske and Subbarow's (1925) method in which  $\alpha$ -aminonaphtholsulphonic acid was used as the reducing agent. Determinations of soluble phosphorus were also performed, but these data are too incomplete to justify presentation here; the methods and results are reported in detail in the original thesis (Grant Lipp 1952).

Owing to the death of certain plants, the later harvests were incomplete to a greater or lesser extent. Even where plants could be harvested, there was not

		•	-
Days from	Source of	Degrees of	Mean Square
Sowing	Variation	Freedom	$ imes 10^{-5}$
11	N	2	756
	Р	2	9270
	K	2	5129
	$N \times P$	4	1552
	$N \times K$	4	2429
	$P \times K$	4	850
	Error	3	1257
22	N	2	1608***
	Р	2	23506***
	К	2	3544***
	$\mathbf{N}  imes \mathbf{P}$	4	319**
	$\mathbf{N} \times \mathbf{K}$	4	125
	$P \times K$	4	609**
	Error	8	44
29	N	3	755
	Р	4	40381***
•	K	3	8539***
	${f N} imes{f P}$	12	795*
	$\mathbf{N}  imes \mathbf{K}$	9	396
	$\mathrm{P} imes\mathbf{K}$	12	1192***
	Error	34	289
37	N	3	834
	Р	4	23298***
	K	3	3335***
	m N  imes P	12	755
	$\mathbf{N}  imes \mathbf{K}$	9	503
	$\mathbf{P}  imes \mathbf{K}$	12	806
	Error	24	400
44	N	3	1837***
	Р	4	27295***
	K	3	4394***
	${f N} imes{f P}$	12	926**
	${ m N} imes{ m K}$	9	270
	$P \times K$	12	1205***
	Error	33	259

TABLE 1 TOTAL PHOSPHORUS CONTENT (PER CENT. OF DRY MATTER) AS AFFECTED BY INITIAL TREATMENTS: ANALYSIS OF VARIANCE

\* P: 0.01-0.05. \*\* P: 0.001-0.01. \*\*\* P < 0.001.

always enough material to permit analysis. In all these cases, "missing plot" values had to be fitted before an analysis of variance was performed; the methods used

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# TABLE 2 PHOSPHORUS CONTENT (PER CENT. OF DRY MATTER): SIGNIFICANT EFFECTS OF INITIAL TREATMENTS

	P1	P <sub>3</sub>	$P_5$
N <sub>1</sub>	0.239	0.465	0.551
$N_3$	0.245	0.376	0.579
$N_5$	0.180	0.329	0.504
K1	0.249	0.447	0.670
$\mathbf{K}_{3}$	0.212	0.390	0.496
$\mathbf{K}_{5}$	0.202	0.333	0.467

# 22 Days from Sowing Interactions between Initial Treatments

29 Days from Sowing Interactions between Initial Treatments

	$P_1$	$P_2$	$P_3$	$P_4$	$P_5$
N <sub>1</sub>	0.146	0.206	0.337	0.458	0.431
$N_2$	0.129	0.140	0.281	0.371	0.530
$N_3$	0.149	0.157	0.227	0.458	0.502
$N_5$	0.118	0.137	0.194	0.370	0.526
$\mathbf{K_1}$	0.155	0 · 201	0.328	0.588	0.678
$\mathbf{K_2}$	0.126	0.154	0.248	0.374	0.442
$\mathbf{K_3}$	0.132	0.152	0.253	0.402	0.426
$\mathbf{K}_{5}$	0.130	$0 \cdot 134$	$0 \cdot 210$	0.292	0.452

# **37** Days from Sowing

Mean Ef	tects at Different I	Levels of Initial	Treatments
$P_1$	0.096	K <sub>1</sub>	0.281
$P_2$	0.126	$\mathbf{K_2}$	0.218
$P_3$	0.200	$\mathbf{K_3}$	0.198
$\mathbf{P_4}$	0.314		
$P_5$	0.377	$\mathbf{K}_{5}$	0.192

#### 44 Days from Sowing Interactions between Initial Treatments

	P <sub>1</sub>	$P_2$	$P_3$	$P_4$	P <sub>5</sub>
N <sub>1</sub>	0.102	0.105	0.276	0.394	0.366
$N_2$	0.066	0.107	0.184	0.266	0.413
$N_3$	0.094	0.114	0.140	0.299	0.440
$\mathbf{N}_{5}$	0.099	0.078	0.144	0.175	0.381
$K_1$	0.086	0.100	0.245	0.392	0.583
$\mathbf{K_2}$	0.084	0.089	0.186	$0 \cdot 245$	0.322
$\mathbf{K_3}$	0.093	0.115	0.172	0.282	0.350
$\mathbf{K}_{5}$	0.099	0.100	0.141	0.215	0.356

for doing this are described in the original thesis (Grant Lipp 1952), where also the results are presented in greater detail. The data for 98 days were too fragmentary to be worth treatment in this way; although we allude to them in the text wherever appropriate, we have on this account not thought it worthwhile to tabulate them.

# III. RESULTS

## (a) Phosphorus Content as Affected by Treatments

### (i) Total Phosphorus Content of Plants

Table 1 presents analyses of variance of the data for total phosphorus content at each harvest, as per cent. of dry matter. The mean values for effects shown to be significant are presented in Table 2, and in appropriate cases solid diagrams have been prepared (Figs. 1–5). The mean phosphorus content fell from 0.96 per cent. in the seed to 0.67 per cent. by 11 days and 0.22 per cent. by 37 days. It still remained at about this level at 44 days, but the rather scanty data for 98 days suggest that it subsequently increased.



Figs. 1-3.—Effect of phosphorus (Fig. 1), potassium (Fig. 2), and nitrogen (Fig. 3) supply on . total phosphorus content at different stages of development.

(1) Mean effects of initial treatments.—From 22 days onwards the effect of phosphorus treatment on phosphorus content was highly significant (Fig. 1). A two- to four-fold increase may be seen from  $P_1$  to  $P_5$ . This effect was already apparent at 11 days, though at that early date it had not reached significance; and the same trend continued to 98 days.

The effect of potassium treatment (Fig. 2) was highly significant from 22 days onwards. There was a marked fall in phosphorus content as the supply of potassium was increased from  $K_1$  to  $K_2$ , but further increases in potassium supply had little or no effect. Differences of the same sort could already be seen at 11 days. There was a large increase in dry weight from  $K_1$  to  $K_2$ , and little or no increase as potassium supply was increased further. The fall in phosphorus content from  $K_1$ to  $K_2$  may thus be regarded as a "dilution" effect.

Nitrogen supply fairly consistently resulted in a decreased phosphorus content (Fig. 3), though this effect reached significance only at 22 and 44 days. This cannot

be explained, like the effect of potassium, in terms of dilution only, since the highest level of nitrogen supply had an adverse effect on yield. This effect of nitrogen on phosphorus content was also apparent in the fragmentary data for the final harvest.

(2) Interactions of initial treatments.—The nitrogen-phosphorus interaction (Fig. 4) reached significance at 22, 29, and 44 days. At all times the main feature of this interaction seems to have been a failure of the highest level of phosphorus supply ( $P_5$ ) to increase phosphorus content where nitrogen was deficient. Where the nitrogen supply was adequate, a progressive increase in phosphorus content occurred throughout the range of phosphorus treatments used. At 22 days, this interaction is somewhat obscured by the absence of analytical data for treatments including  $P_4$  (the optimum for phosphorus content where nitrogen supply was low); but the data available are quite consistent with this interpretation based on later harvests. At 98 days, too, the results, though in themselves hardly adequate as a basis for firm conclusions, support those derived from fuller data of earlier harvests.



Fig. 4.—Interaction effects of nitrogen and phosphorus supply on total phosphorus content.

The phosphorus-potassium interaction (Fig. 5) was also highly significant at 22, 29, and 44 days. This interaction shows itself in a more marked influence of potassium supply on phosphorus content at the higher levels of phosphorus supply; there is an accumulation of phosphorus with increasing phosphorus supply when growth is restricted by potassium deficiency ( $K_1$ ). Conversely, where phosphorus supply is limiting, potassium deficiency does not result in any appreciable accumulation or "luxury consumption" of phosphorus. At 98 days, the data available are insufficient to show this interaction.

At no stage does the interaction between nitrogen and potassium effects approach significance.

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(3) Subtreatment effects.—Analytical data at 98 days are too incomplete to allow any firm conclusions to be reached, but at least it may be said that supplementary phosphorus at 46 days increased the content of phosphorus in plants initially receiving a low supply of this element. No general effect of supplementary nitrogen or potassium on phosphorus content was recognizable.

## (ii) Total Phosphorus Content of Separated Organs

As already indicated, the plants harvested at 44 days were divided into younger and older leaves wherever they were large enough, and the latter were further divided into laminae and midribs. These organs were analysed separately, and the data thus available covered 24 initial treatments—unfortunately excluding all the low-phosphorus treatments, in which the plants were too small for separation. The data for midribs were incomplete even within this limited range of treatments; the data for the other separated organs were subjected to analysis of variance, the results of which are presented in Table 3. Table 4 presents the means for the major differences observed.



Fig. 5.—Interaction effects of potassium and phosphorus supply on total phosphorus content.

There were fairly consistent differences in the phosphorus content of the different organs, the younger leaves containing nearly twice as much (on a dry weight basis) as the older leaf laminae, while the midribs contained even less than the latter (for those treatments for which full data were available, the means were respectively 0.480, 0.286, and 0.203 per cent.). In the effects of treatments, however, the organs did not differ greatly from one another, or from the aerial parts as a whole. The increase in phosphorus supply from P<sub>3</sub> to P<sub>5</sub> led to a very substantial increase in the phosphorus content of all parts, while supply of potassium decreased the phosphorus content—perhaps rather more markedly in the older than the younger leaves.

	Source of Variation	Degrees of Freedom	Mean Square
Younger leaves	N	3	0.0040
	Ρ	1	0.7643***
	К	2	0.1326**
	${ m N}  imes { m P}$	3	0.0330
	$\mathbf{N} \times \mathbf{K}$	6	0.0075
	$\mathbf{P}  imes \mathbf{K}$	2	0.0132
	Error	6	0.0113
Older leaf laminae	N	3	0.0026
	Р	1	0.3673***
	К	2	0.0690**
	$N \times P$	3	0.0197
	$\mathbf{N}  imes \mathbf{K}$	6	0.0038
	$\mathbf{P}  imes \mathbf{K}$	2	0.0279*
	Error	6	0.0048

#### TABLE 3

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TOTAL PHOSPHORUS CONTENT (PER CENT. OF DRY MATTER) OF SEPARATED ORGANS AT 44 DAYS: ANALYSIS OF VARIANCE

* P: $0.01-0.03$ . ** P: $0.001-0.01$ . *** P <	< 0.001.
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#### TABLE 4

TOTAL PHOSPHORUS CONTENT (PER CENT. OF DRY MATTER) OF SEPARATED ORGANS AT 44 DAYS

#### Younger Leaves

Mean Effects at Different Levels of Initial Treatments							
Ν,	0.468			к.	0.610		

$\mathbf{N}_{1}$	0.408			$\mathbf{n}_1$	0.010
$N_{2}$	0.493				
$N_3$	0.431	$P_3$	0.284	K <sub>3</sub>	0.402
$N_5$	0.456	$P_5$	0.640	$K_5$	0.374

Older Leaf Laminae

Mean	Effects	$\mathbf{at}$	Different	Levels	of	Initial	Treatments	

N <sub>1</sub>	0.252			.K1	0.376
N <sub>3</sub>	0.280	P <sub>3</sub>	0.146	K <sub>3</sub>	0.224
N <sub>5</sub>	0.251	$P_5$	0.393	$\mathbf{K}_{5}$	0.208

#### Interactions between Initial Treatments

	K1	${ m K_3}$	${ m K}_5$	
$P_3$	0.184	0.136	0.117	
$\mathbf{P}_{5}$	0.568	0.312	0.300	

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#### (b) Phosphorus Uptake

The amount of phosphorus in the tops (or, at 11 days, in the whole plants) was calculated from the data for dry weight and per cent. phosphorus in plants receiving the 1, 3, and 5 levels of each nutrient. These figures provide an indication of the rate of uptake from the substrate, the error introduced by failure to include the roots in later harvests being small.

The course of phosphorus uptake with different levels of phosphorus supply is shown in Figure 6. During the first 11 days, the plants were growing at the expense of phosphorus stored in the seed, for in no treatment was the phosphorus contained in the plants at the first harvest appreciably more than that in the seed.



Fig. 6.—Course of uptake of phosphorus.

By 22 days, those receiving the larger amounts of phosphorus had begun to make use of them, but the plants from the  $P_1$  treatments were still existing entirely on seed phosphorus. The decrease here may be accounted for by the phosphorus in the roots, which were included at 11 days but not at later stages. Uptake by plants in the  $P_1$  treatments continued to be slow, so that even after 98 days the amount in the plants did not exceed four times the seed content, unless supplementary phosphorus had been supplied at 46 days. Even at this extreme level of deficiency, over half of the phosphorus supplied remained unabsorbed; presumably the root system was so small that the medium could not be effectively explored.

Examination of the data for phosphorus uptake and dry weight accumulation emphasizes the phosphorus starvation of the plants under the  $P_1$  treatments. Thus, with  $P_1$ , dry weight per plant increased by a factor of 10 and phosphorus content per plant only by a factor of five between 22 and 44 days, and consequently the phosphorus concentration in the plant tissue decreased to half its value over the same period. On the other hand, with  $P_5$ , phosphorus uptake and growth kept nearly in step; both increased about 30-fold, and the phosphorus content declined only slightly over this period.

Generally, increased supplies of nitrogen and potassium resulted in increases in phosphorus uptake, especially at the higher levels of phosphorus supply, by allowing greater growth to take place. Uptake was not reduced to the same extent as dry weight by supra-optimal levels of these nutrients.

Nitnomen	Potassium Levels	Phosphorus Levels							
Levels		P <sub>1</sub>	P <sub>2</sub>	P3	$P_4$	$P_5$			
N <sub>1</sub>	K1	+895	-175	-136	-134	-222			
	$\mathbf{K_2}$	+730	+993	+961		-794			
	$K_3$	+1033	+39	+33	-190	-342			
	$\mathbf{K}_{5}$	+740	+518	-378	-205	-101			
$N_2$	K <sub>1</sub>	+77	+152	+ 444		-559			
_	$\mathbf{K_2}$	+1580	+665	+1786	-1166	-692			
	$\mathbf{K_3}$	+1463	+2141	+4246	+532	-1294			
	${ m K}_5$	+1492	+3972	+2065	-1170	-63			
N <sub>3</sub>	K1	+225	+3737	+676	+170	-71			
	$\mathbf{K_2}$	+1991	+1786	+967	-	+237			
	$\mathbf{K_3}$	+1147	+2280	+220	-530	-3192			
	$\mathbf{K}_{5}$	+7486	+1780	+3366	-1355	+1616			
N <sub>5</sub>	K <sub>1</sub>	+281	+370	+82	-9	-136			
-	$\mathbf{K_2}$	-88	+111	+451	+645	+322			
	K <sub>3</sub>	+2	+829	+2446	-2033	-1431			
	$\mathbf{K}_{5}$	+519			+4605	+2567			

TABLE 5 GROWTH RESPONSE TO PHOSPHORUS (MG)

As already mentioned, the total amount of phosphorus removed from the medium by plants receiving the  $P_1$  treatments did not exceed 1 mg per pot—i.e. half the amount supplied. At higher phosphorus levels, the proportion of the phosphorus supplied that was taken up by the plants was less, and rarely reached 20 per cent.

#### (c) Relationship between Growth Response to Phosphorus and Chemical Composition

Responses to the phosphorus subtreatment were estimated, for each initial treatment, by the difference in dry weight between the plant receiving this sub-treatment and its control (Table 5). These differences were corrected for the differences in dimensions of the two plants at the time of applying the subtreatment, as described previously (Goodall *et al.* 1955).

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Regression methods were then used to study the extent to which analytical data could be used to predict the responses to the phosphorus subtreatment. Besides the figures for phosphorus content reported in this paper, data on nitrogen (Slater and Goodall 1957) and potassium (Grant Lipp 1952) were also available. Since material from treatments including  $N_4$  and  $K_4$  had not been analysed, only 80 initial treatments came into consideration; and of these a few could not be used in the regression study because data for dry weight were missing, either for the subtreatment or the control, or because the analytical data included fitted values.

#### TABLE 6

# ANALYSIS OF VARIANCE OF THE REGRESSION OF RESPONSE ON THE COMPOSITION OF ENTIRE AERIAL PARTS

The mean square for reduction due to regression was tested in each case against the residual mean square for that regression. The effect of reducing predicting variables from three to two (or to one), given by the difference in the sum of squares due to regression divided by one (or two) degrees of freedom, can be tested against the residual mean square fitting N, P, and K

		29 Days		37 Days		44 Days	
Reduction due to Regression on:	Degrees of Freedom	$egin{array}{c} { m Sum of} \ { m Squares} \  imes 10^{-4} \end{array}$	$\begin{array}{c} {\rm Mean}\\ {\rm Square}\\ \times 10^{-4} \end{array}$	$egin{array}{c} { m Sum of} \ { m Squares} \  imes 10^{-4} \end{array}$	$egin{array}{c} Mean\ Square\  imes 10^{-4} \end{array}$	$egin{array}{c} { m Sum of} \ { m Squares} \  imes 10^{-4} \end{array}$	$egin{array}{c} Mean \ Square \  imes 10^{-4} \end{array}$
N, P, and K	3	3390	1130**	3675	1225**	4365	1455***
N and P	2	3372	1686**	3430	1715**	3639	1820***
N and K	2	2747	1373**	1270	635	1933	966*
P and K	2	3278	1639**	3470	1735**	3682	1841***
N alone	1	2743	2743**	1005	1005*	422	422
P alone	1	3266	3266***	3386	3386***	3211	3211***
K alone	1	120	120	715	715	1929	1929**
Residue fitting N, P, and K	63	14994	238	14709	234	14019	223

\* P: 0.01-0.05. \*\* P: 0.001-0.01. \*\*\* P < 0.001.

(i) Total Phosphorus.—At 29, 37, and 44 days, where a substantial number (67) of complete sets of data was available, the regression of response on the total phosphorus content of the aerial parts was highly significant (see Table 6), and the closeness of this relationship did not change with time. The significant regressions on nitrogen content may be ascribed to the close relationship between nitrogen and phosphorus content in the earlier harvests. At 44 days the simple regression on potassium content was also significant. The contribution to the multiple regression from nitrogen and potassium content did not reach significance at any stage; this contribution increased, however, as the time of sampling approached that at which the subtreatment was applied, and at 44 days it was probably too large to ignore safely. This contribution falling just short of significance cannot, however, be ascribed either to nitrogen or to potassium separately.

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The equations for the simple regressions on phosphorus content are: for 29 days

$$y = 1987 - 4220 x_P,$$

for 37 days

$$y = 1954 - 5350 x_P$$

and for 44 days

 $y = 1812 - 4967 x_P$ 

while the multiple regression on the content of all three nutrients at 44 days is:

 $y = -415 + 636 x_N - 5786 x_P + 224 x_K$ 

where y is the response in mg, while  $x_N$ ,  $x_P$ , and  $x_K$  represent the content of the three elements in the plant material (per cent. of dry matter).

# TABLE 7 ANALYSIS OF VARIANCE OF THE REGRESSION OF RESPONSE ON THE COMPOSITION OF DIFFERENT PLANT PARTS AT 44 DAYS

Reduction	Degrees	Laminae of Older Leaves		Midribs of Older Leaves		Younger Leaves		Entire Aerial Parts	
due to	of								
Regression on:	Freedom	Sum of	Mean	Sum of	Mean	Sum of	Mean	Sum of	Mean
		Squares	Square	Squares	Square	Squares	Square	Squares	Square
		$ imes 10^{-4}$	×10-4	$ imes 10^{-4}$	$ imes 10^{-4}$	$\times 10^{-4}$	$ imes 10^{-4}$	$ imes 10^{-4}$	$ imes 10^{-4}$
N, P, and K	3	2134	711	1656	552	1731	577	2058	686
N alone	1	82	82	5	5	325	325	70	70
P alone	1	1256	1256*	982	982	1480	1480*	1299	1299*
K alone	1	1452	1452*	675	675	436	436	1006	1006
Residue fitting N, P, and K	28	7322	262	7801	279	7725	276	7398	264

\* P: 0.01-0.05.

At 11 and 22 days the number of complete sets of data available was much smaller (19), and the regressions did not reach significance. This does not, however, imply that prediction of response from analysis at this early stage is necessarily inferior to that from analyses at 29 days or later; when corresponding small sets of data were used for these later dates of sampling, the regressions again failed to reach significance.

(ii) Choice of Organ.—Regressions similar to those on the analytical data for the entire aerial parts were also computed using analyses of the separated organs at 44 days (Table 7). Unfortunately, only 32 complete sets of data could be used and these did not include treatments with  $P_1$  and  $P_2$  where responses were most marked. Nevertheless, the regression on phosphorus content was significant both for the laminae of the older leaves and for the entire young leaves, and in the latter case was slightly more significant than that on the analyses for the aerial parts as a

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whole, when the corresponding set of data was used. The regression equations are: for laminae of older leaves

	$y = 1456 - 4139 x_P,$
for younger leaves	
	$y = 1832 - 3212 x_P,$
and for entire aerial parts	
	$y = 1603 - 4282 x_P.$
In the compared organs, the	no mag no ovidence t

In the separated organs, there was no evidence that the nitrogen or potassium content affected the relationship between phosphorus content and response.

	CONTENT AT DIFFERENT TIMES						
	Degrees	Mean Square $\times 10^{-3}$					
	of Freedom	29 Days	37 Days	44 Days			
Linear regression	1	29401***	30147***	26669***			
Parabolic term	1	6960	4854	4785			
Remainder	70	2147	2167	2217			

TABLE 8 CURVILINEAR REGRESSIONS OF PHOSPHORUS RESPONSE ON PHOSPHORUS

\*\*\* P < 0.001.

# IV. DISCUSSION

In view of the very marked effects of phosphorus treatment on growth, it was to be expected that the phosphorus content of the tissue should be increased. In fact, it was approximately quadrupled by the highest level of treatment at the later harvests, as compared with  $P_1$ . The increase was already quite marked at 22 days; the suggestion in the figures for 11 days (0.56 per cent. phosphorus for  $P_1$  treatments, 0.76 per cent. phosphorus for  $P_5$  treatments) that a similar difference existed at this early stage must probably be discarded since the total phosphorus in the plant at that time hardly exceeded the seed content.

Addition of the other nutrients usually reduced the phosphorus content of the tissue. In the case of potassium this reduction may clearly be interpreted as an effect of increased growth, for both changes ceased at the same level of potassium supply, and the decrease in phosphorus content did not occur where phosphorus supply was itself the main factor controlling growth. In the case of nitrogen some more direct effect on phosphate uptake would appear also to be involved, since one can point to several instances where the increase in nitrogen supply from the N<sub>3</sub> to the N<sub>5</sub> level has resulted in a decrease both in dry weight and in phosphorus content.

#### NUTRITIONAL INTERACTION IN THE LETTUCE. IV

Whereas an efficient forecast of the response to supplementary nitrogen required data for leaf phosphorus as well as nitrogen (Slater and Goodall 1957), phosphorus content alone formed an adequate basis for forecasting the response to supplementary phosphorus. In considering this difference, however, it must be remembered that phosphorus effects were preponderant throughout the investigation; one may surmise that, if the nitrogen treatments had covered a wider range, information on the nitrogen content of the leaves might well have added to the precision with which responses to phosphorus could be forecast. Lundegårdh (1941, 1951) found this to be true in oats—a given phosphorus content indicated smaller responses to phosphorus if associated with low nitrogen figures than with higher ones.



Fig. 7.—Response to phosphorus as a function of phosphorus content.

It was shown (Slater and Goodall 1957) that the relationship between nitrogen response and leaf composition was curvilinear; in oats, Lundegårdh (1941, 1951) found the same to be true for phosphorus responses. The possibility that the relationship between phosphorus responses and phosphorus content was also curvilinear in the present data was likewise tested. It was found that, in this case, a quadratic equation did not fit the data significantly better than a linear one. The results are presented in Table 8, in the form of analyses of variance.

The regression lines for the three dates of sampling are shown in Figure 7; they lead to the following critical values for phosphorus content, above which no positive response to phosphorus supply may be expected: 29 days, 0.471 per cent. phosphorus; 37 days, 0.365 per cent. phosphorus; and 44 days, 0.365 per cent. phosphorus.

Data for the phosphorus content of different organs, and for soluble phosphorus, were rather scanty, but did not suggest that they would have provided a better

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forecast of phosphorus response than the total phosphorus content of the tops as a whole. In particular, the data for midribs seemed to form, if anything, an inferior index—in contradistinction to the claims often made (e.g. Emmert 1935) that these organs, containing a large proportion of conducting tissue, should provide a particularly good basis for estimating nutrient status.

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