

# NUTRITION OF *HEVEA BRASILIENSIS*

## III. THE INTERRELATIONSHIPS OF MAGNESIUM, POTASSIUM AND PHOSPHORUS

By

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*Seedlings of Hevea brasiliensis, clone Tjirandji 1, were grown in pot sand culture at varying levels of magnesium, potassium and phosphate supply. A close interrelationship between these three nutrients was demonstrated which affected the growth and composition of the plant. Concentrations of rubber in stems and petioles varied slightly with nutrient levels, and were inversely related to the dry weight values. Points of practical importance arising from the results are discussed.*

It has been assumed that the interveinal yellowing frequently observed in leaves of *Hevea brasiliensis* was due to magnesium deficiency, as discussed in the annual reports of the Soils Division for 1949, 1950 and 1952. This view has been confirmed not only by pot culture investigations which have established the appearance of magnesium deficiency symptoms (BOLLE-JONES 1954b) but also by the recent results of field experiments in which the addition of magnesian limestone to affected areas cured the deficiency. This interveinal yellowing, due to magnesium deficiency, is of widespread occurrence in Malaya.

The largest positive growth response of *Hevea brasiliensis* trees to fertilisers in the field is usually obtained on the application of phosphate (HAINES and CROWTHER 1940; AKHURST and OWEN 1950; CONSTABLE and HODNETT 1953), which is, in consequence, regularly applied. This fact, taken in conjunction with the widespread occurrence of magnesium deficiency, suggested that a study of the effects of varying levels of magnesium and phosphate supplies on the growth and composition of *Hevea brasiliensis* in sand culture was necessary.

Neither DE HAAN (1950) nor RHINES, MCGAVACK and LINKE (1952) found any relation between the phosphorus status of *Hevea brasiliensis* and the magnesium content of the leaves but BOLLE-JONES (1954b) reported that laminae of phosphorus deficient plants possessed a low magnesium content. For crops other than *Hevea brasiliensis* some of the published evidence suggested that uptake of phosphorus was positively correlated with magnesium supply or content (BEESON, LYON and BARRENTINE 1944; TRUOG, GOATES, GERLOFF and BERGER 1947; TUCKER and SMITH 1952) while other reports (CHAPMAN 1953; EAVES and KELSALL 1954) indicated that high phosphorus supplies caused magnesium deficiency to appear.

Magnesium deficient laminae of *Hevea brasiliensis* contained more potassium than healthy laminae (DE HAAN 1950; RHINES *et alii* 1952; BOLLE-JONES 1954b) and a negative correlation existed between both minerals in the leaf (BEAUFILS 1954); laminae of plants of low potassium status contained more magnesium (DE HAAN 1950; RHINES *et alii* 1952; BOLLE-JONES 1954b) and more phosphorus (CHAPMAN 1941; RHINES *et alii* 1952; BEAUFILS 1954; BOLLE-JONES 1954b) than healthy laminae. For other crops the inverse relationship between magnesium and potassium was evident in reports by BOYNTON and BURRELL (1944), WALSH and O'DONOHUE (1945), KIDSON (1947), CAIN (1948, 1953), MERRILL, POTTER and BROWN (1953) and MULDER (1952) and the positive effect of potassium deficiency on phosphorus accumulation was observed by WALL (1940), WALLACE and BEAR (1949) and EVANS, LATHWELL and MEDERSKI (1950).

Hence it was obvious that any study of the interrelationship of magnesium and phosphorus in *Hevea brasiliensis* must take into consideration the potassium status of the plant. Accordingly a factorial experiment was designed in which Tjirandji 1 seedlings were grown in sand culture at three different levels of each of magnesium, potassium and phosphate; the growth and composition of these seedlings were examined at intervals.

A preliminary report of this investigation has been given elsewhere (BOLLE-JONES 1954c).

## EXPERIMENTAL

There were 27 treatments, each of which was derived from a different combination of the following magnesium (Mg), potassium (K) and phosphate (P) levels.

Mg<sub>1</sub>, K<sub>1</sub>, P<sub>1</sub> 0.5 milligram equivalents/litre

Mg<sub>2</sub>, K<sub>2</sub>, P<sub>2</sub>, 2.0 milligram equivalents/litre

Mg<sub>3</sub>, K<sub>3</sub>, P<sub>3</sub> 8.0 milligram equivalents/litre

Each treatment or 'plot' consisted of three pots and was carried out in duplicate. Twelve 'selfed' Tjirandji 1 seeds were sown in each pot on 10 February 1953. Later (9 March) when the seeds had germinated the seed residue was carefully excised and removed from each seedling so that the plant became completely dependent on minerals supplied to it in the nutrient solution. Complete plants were removed from each pot and the total dry weight of shoots and roots recorded on the following dates: 21 April; 12 May; 24 June; 28 July; 2 October (final sampling).

Fully expanded laminae from which the midribs were excised and discarded were taken from different whorl positions and analysed for chlorophyll and mineral concentrations; the uppermost leaf whorl is always designated as the top whorl while the successive lower one is referred to as the second. The stems and petioles of plants sampled from a plot, with the exception of the July sampling, were bulked together prior to drying, milling and

rubber extraction; for the July sampling the procedure was similar but the green part only of the stems was bulked with the petioles prior to milling and extraction.

The pots, the cold acid leaching of the sand and the analytical procedures employed have been described (BOLLE-JONES 1954a). Tapwater was used for the preparation of the nutrient solutions. Calcium, nitrate and iron were applied at 4.0, 7.0 and 1.0 milligram equivalents per litre respectively to each treatment. Unavoidable variation in  $\text{Na}^+$  and  $\text{SO}_4^{--}$  concentrations occurred. The  $\text{Na}^+$  concentration ranged between 1 and 8 meq/l and generally decreased with either Mg or K but increased with P level. The  $\text{SO}_4^{--}$  concentration ranged between 3 to 12.5 meq/l and increased with either Mg or K level; phosphate level did not markedly affect it. The micronutrients were supplied in concentrations already reported (BOLLE-JONES 1954a).

The numerical data are presented in the form of two way tables which facilitate the ready inspection of the overall trends and the interpretation of interaction effects; included in each table is the respective standard error.

## RESULTS

### VISUAL OBSERVATIONS

The tallest plants at the end of the experiment grew in the  $\text{Mg}_1\text{K}_2\text{P}_2$  treatment (113 cm) and the smallest in the  $\text{Mg}_3\text{K}_2\text{P}_2$  (82 cm). Increased magnesium level, initially, produced an increase in height but later it generally depressed elongation except in the  $\text{K}_3$  plants in which an increase was still obtained. Increased potassium level generally decreased the height, especially in the  $\text{Mg}_1$  plants; this effect was not always linear as some increase was obtained at the  $\text{K}_2$  level. Phosphate addition markedly decreased the height in the  $\text{Mg}_1\text{K}_3$  treatments.

Increased magnesium supply produced an overall increase in the number of leaflets per plant; this effect was most marked in the higher K and P treatments. Potassium addition decreased the number of leaflets, especially those of the  $\text{Mg}_1$  plants. Phosphate addition produced an overall increase in the number of leaflets; this effect was well marked at the lower K levels. Neither the number of leaflets nor the height measurements are presented here.

Magnesium deficiency symptoms (BOLLE-JONES 1954b) first appeared (April) at the  $\text{P}_3$  level in the midstem leaves of the  $\text{Mg}_1\text{K}_2$  and  $\text{Mg}_1\text{K}_3$  plants (*Figure 1*); later (May) it became apparent at all phosphate levels of these treatments but remained more severe at the higher P levels (*Figure 2*). Less severe symptoms were observed in the  $\text{Mg}_2\text{K}_3$  plants at a later date. Magnesium deficiency was not observed in the  $\text{Mg}_3$  plants; thus the symptoms were mainly confined to the lower Mg levels of the higher K and P treatments (*Figures 1 and 2*).



Figure 1. The effect of increased potassium level on the incidence of magnesium deficiency in the  $Mg_1P_3$  treatments, August:  $Mg_1K_1P_3$ , low potassium (left) and  $Mg_1K_3P_3$ , high potassium (right). Note: (i) chlorotic mottling and tip scorch in midstem laminae of  $K_1$  plant ascribed to potassium deficiency and possibly slight iron deficiency effects, and (ii) marked interveinal yellowing near midribs of lower laminae of  $K_3$  plant due to the initiation of magnesium deficiency.

Symptoms tentatively ascribed to potassium deficiency first appeared (early May) in the high magnesium-low potassium plants as a yellowish mottling of the lower whorl laminae followed by a tip and marginal scorch; these symptoms were soon obvious at all Mg levels (Figure 3). The scorching effects were largely confined to the low potassium-high phosphate treatments at all magnesium levels (October). The mottling was probably contributed to in some degree by iron deficiency effects but where these latter effects were obvious (as in the  $K_1P_3$  treatments) they usually appeared in the top whorl as a marked chlorosis.

Phosphorus deficiency was manifested (late May) as a purplish tinting of the underside of the younger or second whorl laminae accompanied by restricted growth and few leaves; these effects were usually less severe at the higher Mg levels (Figure 3). This was later (September-October) followed, in severe instances, by a necrosis of the leaf tip which turned upwards and frequently became twisted, while the margins inrolled towards the upper surface (Figure 4). The tinting effect did not necessarily precede the other symptoms on the same lamina but both generally occurred on the same plant. Both types of symptom were first observed in the  $P_1$  treatments with a tendency to appear first at the  $Mg_1$  level. The tip necrosis and upward curling, although associated with a low phosphate supply and related to phos-

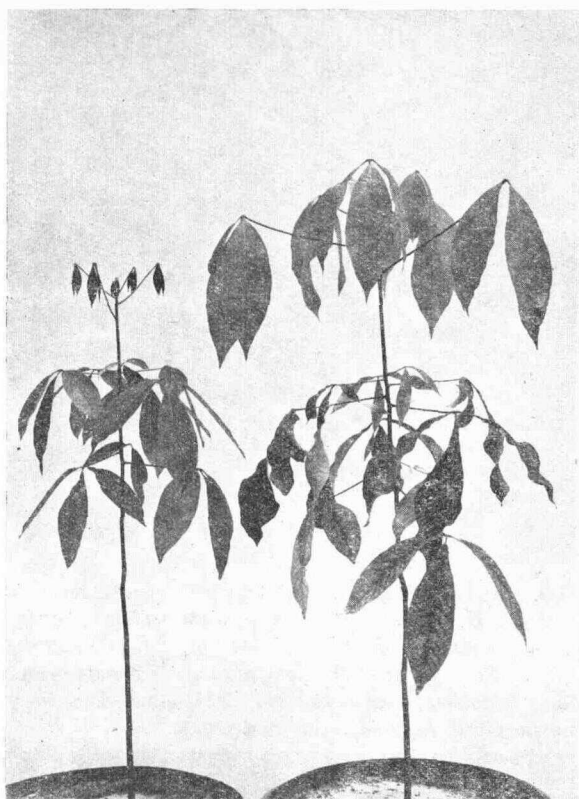


Figure 2. The effect of increased phosphate level on the incidence of magnesium deficiency in the  $Mg_1 K_2$  treatments, August:  $Mg_1 K_2 P_1$ , low phosphate (left) and  $Mg_1 K_2 P_2$ , normal phosphorus (right). Note: (i) mild phosphate deficiency of  $P_1$  plant, and (ii) severe magnesium deficiency in lower leaves of  $P_2$  plant.

phorus deficiency tinting effects, may however be directly due to an induced deficiency of calcium, but as deficiency symptoms of the latter have not been established the uncertainty remains.

An interesting example of the effect of nutrient level variation on the metabolism of *Hevea brasiliensis* was the effect of K level on the  $Mg_1 P_1$  plants. Thus when potassium was applied at the  $K_2$  level marked phosphorus deficiency and slight magnesium deficiency effects occurred but at the  $K_3$  level magnesium deficiency was predominant.

#### TOTAL DRY WEIGHT PER PLANT (SHOOT + ROOT)

TABLE I—The addition of magnesium produced an overall increase in the dry weight of the plants for the earlier months (up until July); this increase was highly significant for both May and June samplings and was especially marked at the  $P_3$  level in June (significant MgP interaction). Later, this increase was apparent in the  $K_3$  treatments only.

Increased supplies of potassium produced an overall decrease in the dry weight; at first this decrease was linear but later the  $K_2$  plants produced a greater dry weight than either the  $K_1$  or  $K_3$  plants. The detrimental effect of potassium addition on dry

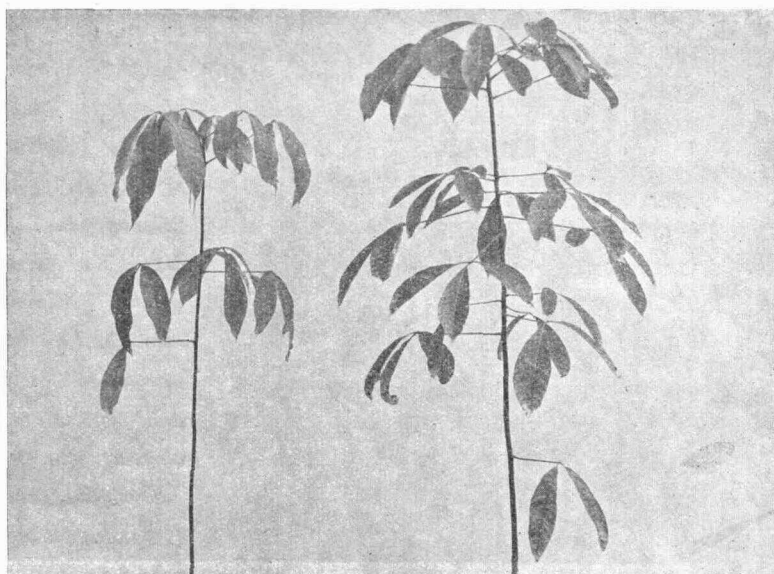


Figure 3. The effect of magnesium level on the vigour of the  $K_1 P_1$  plants, September:  $Mg_1 K_1 P_1$ , low magnesium (left) and  $Mg_2 K_1 P_1$ , normal magnesium (right). Note: (i) 'thin' small leaved appearance of  $Mg_1$  plant mainly due to phosphorus deficiency, and (ii) more vigorous appearance of  $Mg_2$  plant and the occurrence of symptoms ascribed to potassium deficiency.



Figure 4.  $Mg_3 K_3 P_1$  plant, late September. Note marginal and tip scorch with inward rolling of the margin and upward turning of lamina tip. Symptoms associated with a severely reduced phosphate status, but possibly partially due to calcium deficiency effects.

TABLE I: TOTAL DRY WEIGHT OF PLANT (SHOOT + ROOT)  
Grams

	April				May				June				July				October							
Level	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean				
Mg <sub>1</sub>	(±0.16)			(±0.09)	(±0.28)			(±0.16)	(±0.58)			(±0.33)	(±2.1)			(±1.2)	(±8.0)			(±4.6)				
Mg <sub>2</sub>	3.1	3.0	2.8	3.0	5.3	4.8	4.0	4.7	14	14	9	12	23	21	9	18	59	69	23	50				
Mg <sub>3</sub>	3.4	3.2	2.9	3.2	5.7	5.8	5.4	5.6	15	16	14	15	22	22	18	21	52	61	44	52				
	3.4	3.2	3.0	3.2	5.7	5.8	5.4	5.6	15	17	14	15	19	22	22	21	47	56	35	46				
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean				
K <sub>1</sub>	(±0.16)			(±0.09)	(±0.28)			(±0.16)	(±0.58)			(±0.33)	(±2.1)			(±1.2)	(±8.0)			(±4.6)				
K <sub>2</sub>	3.4	3.4	3.1	3.3	5.8	6.2	4.7	5.6	14	16	14	14	18	25	23	22	47	56	54	52				
K <sub>3</sub>	3.2	3.3	2.8	3.1	5.5	5.9	4.9	5.4	14	17	15	16	21	22	22	22	54	67	65	62				
	2.9	2.9	2.9	2.9	5.0	5.5	4.3	4.9	13	13	12	12	15	16	17	16	33	41	27	34				
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean				
P <sub>1</sub>	(±0.16)			(±0.09)	(±0.28)			(±0.16)	(±0.58)			(±0.33)	(±2.1)			(±1.2)	(±8.0)			(±4.6)				
P <sub>2</sub>	3.0	3.1	3.4	3.2	5.0	5.6	5.6	5.4	13	14	14	14	18	16	20	18	39	50	46	45				
P <sub>3</sub>	3.1	3.1	3.4	3.2	5.4	5.7	6.5	5.9	13	16	16	15	18	23	22	21	68	50	45	55				
	2.9	3.3	2.7	3.0	3.8	5.4	4.7	4.6	10	15	16	14	17	23	22	21	44	56	46	49				
Sig. effects	P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01					
Linear	K				K				Mg, P				Mg, K				Mg				K			
Quadratic	—				Mg				P				Mg, K, P				—				K			
Overall	K, Mg × P		—		K		Mg, P		Mg × P		Mg, K, P, Mg × K		K, Mg × K				K							

weight was usually far more severe in the  $Mg_1$  treatments than in the  $Mg_3$  (significant MgK interaction).

Phosphate addition generally produced an overall decrease in dry weight for the earlier months; this effect usually varied with Mg level (significant MgP interaction). Later, the  $P_2$  and  $P_3$  plants gained considerably in weight and increases with phosphate level were obtained.

#### RUBBER CONCENTRATION IN STEMS AND PETIOLES

TABLE II—The effect of increased nutrient level on rubber concentration was not always consistent from month to month.

The addition of magnesium decreased the concentration of rubber for the earlier months (April, May); this decrease was significant at the May sampling. No consistent effect of magnesium level was apparent in June and July but a slight overall increase was obtained in October.

The addition of potassium produced an overall increase in rubber concentration in the April, May and June samplings; this effect was significant for April and June. Later (October) potassium addition produced a decreased concentration.

A significant increase in rubber concentration due to phosphate addition was obtained in June and July; the phosphate effect was more marked at the lower Mg levels and this resulted in a significant MgP interaction.

#### CHLOROPHYLL CONCENTRATION IN THE LAMINAE

TABLE III—Increased levels of magnesium usually produced an overall increase in chlorophyll concentration although opposite trends were noted for the top whorl laminae of the June and July samplings. This positive effect of magnesium was significant for both second and third whorl laminae in May.

In general, with the exception of the October sampling, increased potassium level produced an overall increase in the chlorophyll concentration. Positive significant effects due to potassium were recorded at all samplings.

Increased levels of phosphate caused reductions in chlorophyll concentration at the earlier samplings (April-June); later samplings revealed a diminution of this effect. The depressive influence of phosphate on chlorophyll concentration was highly significant for the second whorl laminae at the June sampling.

#### MINERAL CONCENTRATIONS IN THE LAMINAE

After removal, the seed residues were analysed. It was found that the seedlings usually removed a higher proportion of potassium and phosphorus (76 per cent and 75 per cent respectively) than of magnesium (52 per cent) from the reserves present in the ungerminated seed. Increased levels of potassium decreased the amounts of magnesium or potassium translocated from the seed whereas increased magnesium levels increased the amount of phosphorus translocated. These variations although



TABLE II: THE CONCENTRATION OF RUBBER IN BULKED STEMS AND PETIOLES WITH EXCEPTION OF JULY SAMPLING WHERE  
'GREEN' PART ONLY OF STEMS BULKED WITH PETIOLES  
*Mg rubber/5 gm dry tissue*

Level	April				May				June				July				October			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
<i>Mg<sub>1</sub></i>	(±2.0)			(±1.1)	(±5.5)			(±3.2)	(±3.6)			(±2.0)	(±3.4)			(±1.9)	(±7.2)			(±4.2)
<i>Mg<sub>2</sub></i>	81	75	81	79	91	97	98	95	61	60	69	63	96	95	93	95	62	54	52	56
<i>Mg<sub>3</sub></i>	75	74	82	77	80	83	91	85	60	69	67	65	95	95	94	95	60	51	54	55
	79	75	77	77	81	87	82	83	56	66	66	62	98	96	97	97	65	59	56	60
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
<i>K<sub>1</sub></i>	(±2.0)			(±1.1)	(±5.5)			(±3.2)	(±3.6)			(±2.0)	(±3.4)			(±1.9)	(±7.2)			(±4.2)
<i>K<sub>2</sub></i>	79	76	81	78	95	76	82	84	55	58	63	59	88	101	100	96	64	53	71	63
<i>K<sub>3</sub></i>	73	73	78	75	92	84	90	89	58	67	70	65	87	101	99	95	61	49	55	55
	80	78	81	80	89	91	90	90	64	65	73	67	90	94	100	95	52	59	51	54
Level	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	Mean	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	Mean	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	Mean	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	Mean	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	Mean
<i>P<sub>1</sub></i>	(±2.0)			(±1.1)	(±5.5)			(±3.2)	(±3.6)			(±2.0)	(±3.4)			(±1.9)	(±7.2)			(±4.2)
<i>P<sub>2</sub></i>	80	76	77	77	105	86	85	92	61	56	60	59	85	83	97	88	60	60	58	59
<i>P<sub>3</sub></i>	77	74	74	75	82	87	82	84	57	65	69	63	98	105	92	98	50	54	57	54
	80	80	80	80	99	81	83	88	72	75	59	68	101	96	102	100	60	52	66	59
<i>Sig. effects</i>	<i>P</i> < 0.05			<i>P</i> < 0.01	<i>P</i> < 0.05			<i>P</i> < 0.01	<i>P</i> < 0.05			<i>P</i> < 0.01	<i>P</i> < 0.05			<i>P</i> < 0.01	<i>P</i> < 0.05			<i>P</i> < 0.01
<i>Linear</i>	—			—	—			<i>Mg</i>	—			<i>K, P</i>	—			<i>P</i>	—			—
<i>Quadratic</i>	<i>P</i>			<i>K</i>	—			—	—			—	—			—	—			—
<i>Overall</i>	<i>P</i>			<i>K</i>	<i>Mg</i>			—	<i>K, P</i>			<i>Mg × P</i>	—			<i>P, Mg × P</i>	—			—

TABLE III: CONCENTRATION OF CHLOROPHYLL IN LAMINA  
Mg chlorophyll/gm dry lamina

(continued opposite)

Level	April 2nd Whorl				May 2nd Whorl				May 3rd Whorl				June Top Whorl			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
	(±0.18)			(±0.10)	(±0.24)			(±0.14)	(±0.29)			(±0.17)	(±0.34)			(±0.20)
Mg <sub>1</sub>	6.7	7.2	7.4	7.1	6.0	6.4	5.5	6.0	6.4	6.0	5.6	6.0	5.0	5.9	4.9	5.3
Mg <sub>2</sub>	7.3	7.2	7.4	7.3	6.3	6.5	6.2	6.3	6.5	6.6	7.1	6.7	4.9	4.7	5.1	4.9
Mg <sub>3</sub>	7.2	7.1	7.5	7.3	6.5	6.8	6.3	6.6	6.4	6.9	6.9	6.7	4.6	5.0	5.0	4.9
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
	(±0.18)			(±0.10)	(±0.24)			(±0.14)	(±0.29)			(±0.17)	(±0.34)			(±0.20)
K <sub>1</sub>	7.1	7.3	6.9	7.1	6.3	6.2	6.1	6.2	6.8	6.5	5.9	6.4	5.3	4.8	4.4	4.8
K <sub>2</sub>	7.2	7.2	7.2	7.2	6.7	6.5	6.5	6.6	6.9	6.4	6.1	6.5	5.4	5.0	5.2	5.2
K <sub>3</sub>	7.9	7.0	7.4	7.4	5.9	6.2	6.0	6.0	6.5	6.3	6.8	6.5	5.2	5.0	4.9	5.0
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean
	(±0.18)			(±0.10)	(±0.24)			(±0.14)	(±0.29)			(±0.17)	(±0.34)			(±0.20)
P <sub>1</sub>	7.5	7.4	7.3	7.4	6.0	6.5	6.4	6.3	6.3	6.8	7.1	6.7	5.7	5.1	5.0	5.3
P <sub>2</sub>	6.8	7.3	7.3	7.1	5.8	6.4	6.7	6.3	6.0	6.7	6.6	6.4	5.3	4.8	4.6	4.9
P <sub>3</sub>	7.0	7.3	7.2	7.2	6.0	6.0	6.5	6.2	5.7	6.7	6.5	6.3	4.8	4.8	4.9	4.8
Sig. effects	P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01	
Linear	K		—				Mg				Mg		—		—	
Quadratic	—		—				K		—		—		—		—	
Overall	K × P		—		Mg, K		—				Mg		—		—	

(continued from opposite)

June 2nd Whorl				July Top Whorl				October Top Whorl				October 2nd Whorl				Level.
<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	
(±0.19)			(±0.11)	(±0.24)			(±0.14)	(±0.32)			(±0.18)	(±0.47)			(±0.27)	<i>Mg</i> <sub>1</sub>
4.2	5.0	4.5	4.6	5.8	6.0	5.7	5.8	6.1	5.4	6.0	5.8	5.8	5.8	4.8	5.5	
4.4	4.3	4.8	4.5	5.2	5.6	5.7	5.5	6.6	5.5	6.2	6.1	5.8	5.9	6.2	6.0	
4.3	4.9	4.9	4.7	5.2	5.8	5.3	5.4	5.9	6.2	6.4	6.1	6.2	5.8	6.0	6.0	
<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	Level
(±0.19)			(±0.11)	(±0.24)			(±0.14)	(±0.32)			(±0.18)	(±0.47)			(±0.27)	
5.1	3.9	3.9	4.3	5.6	5.1	5.4	5.4	5.6	7.2	6.0	6.2	6.0	5.9	6.0	6.0	<i>K</i> <sub>1</sub>
5.4	4.6	4.2	4.7	5.7	5.8	6.0	5.8	6.0	5.3	5.7	5.7	6.1	5.4	6.0	5.8	<i>K</i> <sub>2</sub>
5.2	4.6	4.4	4.7	5.4	5.7	5.5	5.6	7.0	5.8	5.8	6.2	5.0	5.5	6.5	5.7	<i>K</i> <sub>3</sub>
<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	Level
(±0.19)			(±0.11)	(±0.24)			(±0.14)	(±0.32)			(±0.18)	(±0.47)			(±0.27)	
5.2	5.4	5.1	5.2	5.6	5.5	5.6	5.6	6.3	6.2	6.2	6.2	5.3	6.1	5.8	5.7	<i>P</i> <sub>1</sub>
4.5	4.1	4.6	4.4	5.8	5.5	5.5	5.6	6.2	6.3	5.8	6.1	5.6	5.6	5.6	5.6	<i>P</i> <sub>2</sub>
4.1	4.0	4.4	4.2	6.1	5.5	5.2	5.6	5.1	5.9	6.5	5.8	5.6	6.3	6.5	6.1	<i>P</i> <sub>3</sub>
<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		Sig. effects
<i>K</i>		<i>P</i>		—		—		—		—		—		—		Linear
<i>P</i>		—		<i>K</i>		—		<i>K</i>		—		—		—		Quadratic
<i>K</i>		<i>P</i>		—		—		—		<i>K</i> × <i>P</i>		—		—		Overall

TABLE IV: CONCENTRATION OF MAGNESIUM IN LAMINA  
% Mg in dry lamina

(continued opposite)

Level	April 2nd Whorl				May 2nd Whorl				May 3rd Whorl				June Top Whorl			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
	(±0.012)			(±0.007)	(±0.01)			(±0.006)	(±0.012)			(±0.007)	(±0.011)			(±0.006)
Mg <sub>1</sub>	.11	.10	.08	.09	.07	.06	.05	.06	.07	.06	.04	.06	.16	.15	.15	.15
Mg <sub>2</sub>	.18	.17	.13	.16	.14	.12	.09	.12	.18	.13	.09	.14	.23	.23	.22	.22
Mg <sub>3</sub>	.40	.35	.27	.34	.29	.24	.21	.25	.47	.37	.26	.37	.35	.34	.29	.33
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
	(±0.012)			(±0.007)	(±0.01)			(±0.006)	(±0.012)			(±0.007)	(±0.011)			(±0.006)
K <sub>1</sub>	.22	.25	.22	.23	.16	.17	.18	.17	.23	.25	.24	.24	.24	.24	.26	.25
K <sub>2</sub>	.22	.19	.20	.20	.14	.14	.14	.14	.17	.19	.20	.19	.22	.24	.25	.24
K <sub>3</sub>	.16	.16	.16	.16	.12	.13	.11	.12	.13	.14	.12	.13	.20	.22	.23	.22
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean
	(±0.012)			(±0.007)	(±0.01)			(±0.006)	(±0.012)			(±0.007)	(±0.011)			(±0.006)
P <sub>1</sub>	.10	.16	.33	.20	.06	.12	.24	.14	.06	.13	.34	.18	.15	.22	.30	.22
P <sub>2</sub>	.09	.16	.35	.20	.06	.12	.27	.15	.05	.14	.40	.20	.15	.22	.33	.23
P <sub>3</sub>	.09	.16	.33	.19	.07	.11	.24	.14	.05	.14	.36	.18	.16	.23	.36	.25
Overall	P < 0.05			P < 0.01	P < 0.05			P < 0.01	P < 0.05			P < 0.01	P < 0.05			P < 0.01
Quadratic	Mg, K				Mg, K				Mg, K				Mg, K, P			
Linear	Mg				Mg				Mg				—			
Sig. effects	Mg, K, Mg, × K				Mg, K				Mg, K				K, P			

(continued from opposite)

June 2nd Whorl				July Top Whorl				October Top Whorl				October 2nd Whorl				Level
$K_1$	$K_2$	$K_3$	Mean	$K_1$	$K_2$	$K_3$	Mean	$K_1$	$K_2$	$K_3$	Mean	$K_1$	$K_2$	$K_3$	Mean	
( $\pm 0.017$ )			( $\pm 0.01$ )	( $\pm 0.015$ )			( $\pm 0.009$ )	( $\pm 0.019$ )			( $\pm 0.011$ )	( $\pm 0.014$ )			( $\pm 0.008$ )	
.07	.03	.02	.04	.13	.15	.13	.14	.14	.12	.12	.13	.08	.06	.02	.05	$Mg_1$
.18	.15	.09	.14	.22	.23	.24	.23	.26	.24	.18	.22	.27	.21	.12	.20	$Mg_2$
.52	.41	.26	.40	.40	.33	.30	.34	.38	.42	.33	.38	.49	.45	.33	.42	$Mg_3$
$P_1$	$P_2$	$P_3$	Mean	$P_1$	$P_2$	$P_3$	Mean	$P_1$	$P_2$	$P_3$	Mean	$P_1$	$P_2$	$P_3$	Mean	Level
( $\pm 0.017$ )			( $\pm 0.01$ )	( $\pm 0.015$ )			( $\pm 0.009$ )	( $\pm 0.019$ )			( $\pm 0.011$ )	( $\pm 0.014$ )			( $\pm 0.008$ )	
.20	.28	.29	.26	.24	.25	.27	.25	.25	.26	.26	.26	.25	.30	.29	.28	$K_1$
.18	.21	.21	.20	.21	.26	.24	.24	.23	.28	.26	.26	.20	.26	.25	.24	$K_2$
.12	.11	.14	.12	.22	.23	.22	.22	.20	.22	.20	.21	.14	.17	.16	.15	$K_3$
$Mg_1$	$Mg_2$	$Mg_3$	Mean	$Mg_1$	$Mg_2$	$Mg_3$	Mean	$Mg_1$	$Mg_2$	$Mg_3$	Mean	$Mg_1$	$Mg_2$	$Mg_3$	Mean	Level
( $\pm 0.017$ )			( $\pm 0.01$ )	( $\pm 0.015$ )			( $\pm 0.009$ )	( $\pm 0.019$ )			( $\pm 0.011$ )	( $\pm 0.014$ )			( $\pm 0.008$ )	
.04	.12	.33	.17	.13	.24	.30	.22	.13	.21	.34	.23	.05	.18	.36	.20	$P_1$
.04	.12	.44	.20	.15	.21	.38	.25	.13	.25	.40	.26	.05	.20	.46	.24	$P_2$
.04	.17	.43	.21	.14	.24	.35	.24	.12	.22	.39	.24	.04	.21	.45	.23	$P_3$
$P < 0.05$		$P < 0.01$		$P < 0.05$		$P < 0.01$		$P < 0.05$		$P < 0.01$		$P < 0.05$		$P < 0.01$		Sig. effects
$Mg, K, P$				$K$		$Mg$		$Mg, K$				$Mg, K, P$				Linear
$Mg$				—		—		—				$K, P$		$Mg$		Quadratic
$Mg, K, P,$ $Mg \times K,$ $Mg \times P$				$Mg \times P$		$Mg, Mg \times K$		$Mg, K$				$Mg, K, P,$ $Mg \times K,$ $Mg \times P$				Overall

TABLE V: CONCENTRATION OF POTASSIUM IN LAMINA  
% K in dry lamina

(continued opposite)

Level	April 2nd Whorl				May 2nd Whorl				May 3rd Whorl				June Top Whorl			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
	(±0.04)			(±0.02)	(±0.05)			(±0.03)	(±0.05)			(±0.03)	(±0.08)			(±0.05)
Mg <sub>1</sub>	1.1	1.3	1.7	1.4	1.2	1.5	2.4	1.7	0.9	1.2	2.0	1.4	1.1	1.7	2.6	1.8
Mg <sub>2</sub>	0.9	1.1	1.4	1.2	0.9	1.3	1.8	1.3	0.7	1.0	1.4	1.0	0.9	1.4	2.1	1.5
Mg <sub>3</sub>	0.8	0.9	1.2	0.9	0.8	1.0	1.3	1.0	0.6	0.8	1.1	0.8	0.9	1.1	1.8	1.2
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
	(±0.04)			(±0.02)	(±0.05)			(±0.03)	(±0.05)			(±0.03)	(±0.08)			(±0.05)
K <sub>1</sub>	1.0	0.9	0.9	0.9	0.9	1.0	0.9	1.0	0.7	0.8	0.7	0.7	1.0	0.9	1.0	1.0
K <sub>2</sub>	1.1	1.1	1.2	1.1	1.2	1.2	1.4	1.3	0.9	0.9	1.1	1.0	1.3	1.4	1.5	1.4
K <sub>3</sub>	1.4	1.4	1.4	1.4	1.8	1.8	2.0	1.8	1.4	1.4	1.7	1.5	1.8	2.4	2.2	2.2
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean
	(±0.04)			(±0.02)	(±0.05)			(±0.03)	(±0.05)			(±0.03)	(±0.08)			(±0.05)
P <sub>1</sub>	1.4	1.2	0.9	1.2	1.6	1.3	1.1	1.3	1.3	1.0	0.8	1.0	1.7	1.3	1.2	1.4
P <sub>2</sub>	1.4	1.2	0.9	1.1	1.7	1.3	0.9	1.3	1.3	1.0	0.8	1.0	1.9	1.6	1.3	1.6
P <sub>3</sub>	1.4	1.1	1.0	1.2	1.8	1.4	1.1	1.4	1.5	1.1	0.9	1.2	1.9	1.4	1.3	1.5
Sig. effects	P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01	
Linear			Mg, K		P		Mg, K				Mg, K, P,		P		Mg, K	
Quadratic	K		—				K		P		K		K			
Overall			Mg, K				Mg, K, Mg × K		K × P		Mg, K, P, Mg × K		P		Mg, K, K × P, Mg × K	

(continued from opposite)

June 2nd Whorl				July Top Whorl				October Top Whorl				October 2nd Whorl				Level
K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	
(±0.06)			(±0.03)	(±0.08)			(±0.04)	(±0.11)			(±0.06)	(±0.07)			(±0.04)	Mg <sub>1</sub> Mg <sub>2</sub> Mg <sub>3</sub>
1.1	1.7	2.6	1.8	1.3	1.9	2.8	2.0	1.4	2.0	2.9	2.1	1.2	1.8	2.6	1.9	
0.8	1.3	2.1	1.4	1.1	1.6	2.2	1.6	1.2	1.4	2.1	1.5	0.9	1.2	1.9	1.4	
0.8	1.0	1.8	1.2	1.1	1.4	1.9	1.4	1.1	1.3	1.9	1.4	0.8	1.0	1.3	1.0	
P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	Level
(±0.06)			(±0.03)	(±0.08)			(±0.04)	(±0.11)			(±0.06)	(±0.07)			(±0.04)	K <sub>1</sub> K <sub>2</sub> K <sub>3</sub>
0.9	0.9	0.9	0.9	1.2	1.1	1.2	1.2	1.2	1.3	1.2	1.2	1.0	1.0	1.0	1.0	
1.2	1.4	1.4	1.3	1.5	1.7	1.7	1.6	1.6	1.4	1.7	1.6	1.3	1.2	1.5	1.4	
1.9	2.2	2.4	2.2	2.1	2.4	2.4	2.3	2.1	2.2	2.5	2.3	1.9	2.0	2.0	2.0	
Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Level
(±0.06)			(±0.03)	(±0.08)			(±0.04)	(±0.11)			(±0.06)	(±0.07)			(±0.04)	P <sub>1</sub> P <sub>2</sub> P <sub>3</sub>
1.7	1.2	1.1	1.3	1.8	1.7	1.4	1.6	2.0	1.5	1.4	1.6	1.8	1.3	1.1	1.4	
1.8	1.5	1.2	1.5	2.1	1.7	1.4	1.7	2.1	1.6	1.2	1.6	1.8	1.3	1.0	1.4	
1.9	1.5	1.3	1.6	2.2	1.6	1.5	1.8	2.2	1.5	1.7	1.8	2.1	1.5	1.0	1.5	
P < 0.05			P < 0.01	P < 0.05			P < 0.01	P < 0.05			P < 0.01	P < 0.05			P < 0.01	Sig. effects
			Mg, K, P	P			Mg, K				Mg, K				Mg, K	Linear
			Mg, K	—			—	K			Mg	K			—	Quadratic
			Mg, K, P, Mg × K, K × P	P, Mg × P			Mg, K, Mg × K	Mg × K			Mg, K				Mg, K, Mg × K	Overall

TABLE VI: CONCENTRATION OF PHOSPHORUS IN LAMINA

% P in dry lamina

(continued opposite)

Level	April 2nd Whorl				May 2nd Whorl				May 3rd Whorl				June Top Whorl			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
	(±0.008)			(±0.005)	(±0.007)			(±0.004)	(±0.008)			(±0.004)	(±0.007)			(±0.004)
Mg <sub>1</sub>	.26	.26	.26	.26	.20	.21	.20	.20	.22	.23	.20	.22	.26	.26	.24	.25
Mg <sub>2</sub>	.24	.24	.24	.24	.19	.19	.18	.19	.21	.22	.20	.21	.25	.25	.23	.24
Mg <sub>3</sub>	.23	.24	.24	.24	.19	.20	.18	.19	.21	.22	.20	.21	.25	.23	.26	.25
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
	(±0.008)			(±0.005)	(±0.007)			(±0.004)	(±0.008)			(±0.004)	(±0.007)			(±0.004)
K <sub>1</sub>	.22	.23	.28	.24	.16	.18	.23	.19	.18	.19	.27	.21	.16	.24	.36	.25
K <sub>2</sub>	.21	.24	.29	.25	.17	.18	.24	.20	.18	.20	.28	.22	.14	.23	.37	.25
K <sub>3</sub>	.22	.24	.27	.24	.16	.18	.21	.18	.17	.19	.25	.20	.15	.24	.34	.24
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean
	(±0.008)			(±0.005)	(±0.007)			(±0.004)	(±0.008)			(±0.004)	(±0.007)			(±0.004)
P <sub>1</sub>	.22	.21	.22	.22	.18	.16	.16	.16	.18	.18	.18	.18	.16	.15	.14	.15
P <sub>2</sub>	.24	.24	.22	.24	.18	.19	.18	.18	.19	.19	.20	.19	.24	.23	.23	.24
P <sub>3</sub>	.30	.28	.27	.28	.25	.22	.22	.23	.28	.26	.26	.27	.35	.34	.38	.36
Sig. effects	P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01	
Linear				Mg, P				Mg, P				P				P
Quadratic	P			—	K, P			—	K, P				P			
Overall	Mg			P	Mg, K			P	K, P				Mg × K			P, Mg × P



(continued from opposite)

June 2nd Whorl				July Top Whorl				October Top Whorl				October 2nd Whorl				Level
<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	<i>K</i> <sub>1</sub>	<i>K</i> <sub>2</sub>	<i>K</i> <sub>3</sub>	Mean	
(±0.009)			(±0.005)	(±0.014)			(±0.008)	(±0.033)			(±0.019)	(±0.017)			(±0.010)	<i>Mg</i> <sub>1</sub>
.22	.21	.21	.22	.26	.25	.26	.26	.27	.22	.25	.25	.23	.22	.23	.22	
.20	.22	.22	.22	.26	.25	.29	.27	.27	.25	.26	.26	.24	.24	.29	.25	
.23	.22	.22	.22	.28	.26	.27	.27	.30	.27	.28	.28	.31	.24	.22	.26	<i>Mg</i> <sub>3</sub>
<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	<i>P</i> <sub>1</sub>	<i>P</i> <sub>2</sub>	<i>P</i> <sub>3</sub>	Mean	Level
(±0.009)			(±0.005)	(±0.014)			(±0.008)	(±0.033)			(±0.019)	(±0.017)			(±0.010)	<i>K</i> <sub>1</sub>
.13	.20	.32	.22	.17	.25	.38	.27	.21	.27	.37	.28	.17	.22	.39	.26	
.13	.20	.31	.22	.18	.26	.32	.25	.18	.22	.34	.25	.17	.20	.32	.23	<i>K</i> <sub>2</sub>
.14	.20	.30	.22	.24	.25	.33	.27	.20	.24	.35	.26	.18	.21	.36	.25	<i>K</i> <sub>3</sub>
<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	<i>Mg</i> <sub>1</sub>	<i>Mg</i> <sub>2</sub>	<i>Mg</i> <sub>3</sub>	Mean	Level
(±0.009)			(±0.005)	(±0.014)			(±0.008)	(±0.033)			(±0.019)	(±0.017)			(±0.010)	<i>P</i> <sub>1</sub>
.14	.13	.13	.13	.18	.23	.18	.20	.20	.19	.20	.20	.17	.17	.17	.17	
.20	.20	.21	.20	.26	.24	.26	.25	.26	.24	.23	.24	.20	.22	.20	.21	<i>P</i> <sub>2</sub>
.31	.31	.32	.31	.33	.33	.37	.34	.29	.34	.42	.35	.30	.37	.40	.36	<i>P</i> <sub>3</sub>
<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>Sig. effects</i>
		<i>P</i>				<i>P</i>				<i>P</i>		<i>Mg</i>		<i>P</i>		<i>Linear</i>
		<i>P</i>		—		—		—		—				<i>P</i>		<i>Quadratic</i>
		<i>P</i>		<i>Mg</i> × <i>P</i>		<i>P</i> , <i>K</i> × <i>P</i>				<i>P</i>		<i>Mg</i> , <i>Mg</i> × <i>K</i> , <i>Mg</i> × <i>P</i>		<i>P</i>		<i>Overall</i>

TABLE VII: CONCENTRATION OF MANGANESE IN LAMINA  
p.p.m. Mn in dry lamina

(continued opposite)

Level	April 2nd Whorl				May 2nd Whorl				May 3rd Whorl				June Top Whorl			
	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
	(±1.6)			(±0.9)	(±3.2)			(±1.9)	(±1.8)			(±1.0)	(±3.0)			(±1.7)
Mg <sub>1</sub>	24	26	30	27	17	18	23	19	27	33	31	30	28	34	44	35
Mg <sub>2</sub>	24	29	28	27	22	16	21	20	28	28	33	30	24	21	26	24
Mg <sub>3</sub>	26	23	25	24	17	15	16	16	29	26	25	27	21	21	23	22
Level	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	Mean
	(±1.6)			(±0.9)	(±3.2)			(±1.9)	(±1.8)			(±1.0)	(±3.0)			(±1.7)
K <sub>1</sub>	22	26	26	25	20	14	21	18	24	28	32	28	19	20	34	24
K <sub>2</sub>	24	27	27	26	14	17	18	17	24	30	32	29	20	20	35	25
K <sub>3</sub>	27	28	28	28	17	19	23	20	28	30	32	30	25	26	42	31
Level	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean	Mg <sub>1</sub>	Mg <sub>2</sub>	Mg <sub>3</sub>	Mean
	(±1.6)			(±0.9)	(±3.2)			(±1.9)	(±1.8)			(±1.0)	(±3.0)			(±1.7)
P <sub>1</sub>	25	25	23	24	17	21	14	17	29	25	22	25	28	19	18	21
P <sub>2</sub>	27	29	25	27	16	17	17	17	30	30	29	29	23	23	19	22
P <sub>3</sub>	29	28	25	27	25	21	17	21	32	34	30	32	54	29	28	37
Sig. effects	P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01		P < 0.05		P < 0.01	
Linear	P		—		—		—		Mg		P		K		Mg, P	
Quadratic	—		—		—		—		—		—		Mg		P	
Overall	—		—		—		—		Mg × K		P		K		Mg, P, Mg × P	

(continued from opposite)

<i>June 2nd Whorl</i>				<i>July Top Whorl</i>				<i>October Top Whorl</i>				<i>October 2nd Whorl</i>				<i>Level</i>
<i>K<sub>1</sub></i>	<i>K<sub>2</sub></i>	<i>K<sub>3</sub></i>	<i>Mean</i>	<i>K<sub>1</sub></i>	<i>K<sub>2</sub></i>	<i>K<sub>3</sub></i>	<i>Mean</i>	<i>K<sub>1</sub></i>	<i>K<sub>2</sub></i>	<i>K<sub>3</sub></i>	<i>Mean</i>	<i>K<sub>1</sub></i>	<i>K<sub>2</sub></i>	<i>K<sub>3</sub></i>	<i>Mean</i>	
$(\pm 3.4)$			$(\pm 2.0)$	$(\pm 3.5)$			$(\pm 2.0)$	$(\pm 1.6)$			$(\pm 0.9)$	$(\pm 3.2)$			$(\pm 1.8)$	<i>Mg<sub>1</sub></i>
32	42	53	42	26	25	51	34	19	21	30	23	26	38	51	38	
25	25	28	26	19	25	26	23	15	14	18	16	22	19	27	22	
22	23	24	23	24	19	20	21	16	18	18	17	22	20	28	23	
<i>P<sub>1</sub></i>	<i>P<sub>2</sub></i>	<i>P<sub>3</sub></i>	<i>Mean</i>	<i>P<sub>1</sub></i>	<i>P<sub>2</sub></i>	<i>P<sub>3</sub></i>	<i>Mean</i>	<i>P<sub>1</sub></i>	<i>P<sub>2</sub></i>	<i>P<sub>3</sub></i>	<i>Mean</i>	<i>P<sub>1</sub></i>	<i>P<sub>2</sub></i>	<i>P<sub>3</sub></i>	<i>Mean</i>	<i>Level</i>
$(\pm 3.4)$			$(\pm 2.0)$	$(\pm 3.5)$			$(\pm 2.0)$	$(\pm 1.6)$			$(\pm 0.9)$	$(\pm 3.2)$			$(\pm 1.8)$	<i>K<sub>1</sub></i>
18	19	42	26	17	19	33	23	15	15	20	17	18	17	35	23	
19	23	49	30	18	16	35	23	15	16	22	18	20	24	33	26	
27	28	49	35	21	30	46	32	16	18	31	22	31	25	49	35	
<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	<i>Mean</i>	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	<i>Mean</i>	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	<i>Mean</i>	<i>Mg<sub>1</sub></i>	<i>Mg<sub>2</sub></i>	<i>Mg<sub>3</sub></i>	<i>Mean</i>	<i>Level</i>
$(\pm 3.4)$			$(\pm 2.0)$	$(\pm 3.5)$			$(\pm 2.0)$	$(\pm 1.6)$			$(\pm 0.9)$	$(\pm 3.2)$			$(\pm 1.8)$	<i>P<sub>1</sub></i>
29	19	16	21	20	18	18	18	19	12	14	15	32	20	17	23	
24	25	21	23	28	18	18	22	20	14	15	17	30	17	19	22	
74	34	32	47	54	33	27	38	30	20	23	24	53	29	34	39	
<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>P</i> < 0.05		<i>P</i> < 0.01		<i>Sig. effects</i>
			<i>Mg, K, P</i>				<i>Mg, K, P</i>				<i>Mg, K, P</i>				<i>Mg, K, P</i>	<i>Linear</i>
<i>Mg</i>		<i>P</i>		<i>P</i>		—				<i>Mg, F</i>				<i>Mg, P</i>		<i>Quadratic</i>
<i>K</i>		<i>Mg, P, Mg × P</i>		<i>Mg × P</i>		<i>Mg, K, P, Mg × K</i>		<i>Mg × K, K × P</i>		<i>Mg, K, P</i>		<i>Mg × K</i>		<i>Mg, K, P</i>		<i>Overall</i>

well defined were slight and never exceeded 5 per cent of the original amount of the element present in the ungerminated seed; full results are not presented here.

**MAGNESIUM, TABLE IV**—The concentration of magnesium in the laminae increased with magnesium and decreased with potassium levels; both effects were highly significant, that of potassium being predominantly linear. Increased magnesium supply was most effective in increasing magnesium content at the  $K_1$  or  $P_2$  and  $P_3$  levels (significant MgK, MgP interactions). The effect of increased phosphate supply was to give an increase in magnesium content at the  $Mg_3$  level. This effect, which was largely responsible for the overall response to phosphate, was sometimes significant.

**POTASSIUM, TABLE V**—The concentration of potassium in the laminae increased with potassium and decreased with magnesium levels; both effects were highly significant, that of magnesium being predominantly linear. Potassium addition was always more effective in increasing the potassium content at the lowest magnesium level (significant MgK interaction). Increased phosphate supply gave an overall increase in potassium concentration; this response was usually significant and was mainly contributed to by the  $K_3$  treatments (significant KP interaction noted in May and June).

**PHOSPHORUS, TABLE VI**—Increased phosphate supply significantly increased the phosphorus concentration in the laminae; this effect was more marked in the  $K_1$  treatments but only in July was the KP interaction found to be significant. At the earlier samplings (April, May) increased magnesium supply produced significant reductions in the phosphorus content of the second whorl laminae but later this effect was reversed. The effect of potassium supply on phosphorus content was not consistent.

**MANGANESE, TABLE VII**—The concentration of manganese in the laminae showed well marked changes due to nutrient level; these effects first became obvious in May and persisted until the end of the experiment. Increased magnesium level decreased the manganese content of the laminae whereas increased supplies of either potassium or phosphate increased it; these effects were highly significant. The positive effects of potassium and phosphate on manganese content were much more pronounced at the  $Mg_1$  level; this resulted in significant MgK and MgP interactions.

## DISCUSSION

The main objective of this investigation was to examine the nature and importance of the interrelationships of magnesium and phosphorus in *Hevea brasiliensis*. It was found that magnesium addition at first reduced the concentration of phosphorus in the lamina but later increased it; phosphate addition frequently enhanced the magnesium concentration of the laminae at higher magnesium levels.

In addition to this direct effect of one exerted upon the other they both influenced the concentration of potassium in the lamina; thus increased magnesium supply invariably decreased the potassium concentration whereas increased phosphate supply increased it at the higher potassium levels. The opposing nature of magnesium and phosphate was also revealed in their effect on the concentrations of manganese and, to a lesser extent, chlorophyll in the lamina. Thus increased magnesium supply decreased the concentration of manganese and increased that of chlorophyll whereas increased phosphate supply increased the manganese and decreased the chlorophyll concentrations.

A relationship between the effects of magnesium and phosphorus in the nutrition of *Hevea brasiliensis* was therefore demonstrated. As observed on page 232 the inverse nature of the interrelationship between magnesium and potassium in both *Hevea brasiliensis* and other crops has been well established. The beneficial effect of magnesium on phosphate uptake has also been reported by some authors (ZIMMERMAN 1947 and *loc. cit.*). The detrimental effect of magnesium addition on manganese accumulation has not, however, been reported in the general literature, although the beneficial influence of potassium addition on manganese uptake has been noted (YORK, BRADFIELD and PEECH 1954). On the other hand BEAUFILS (1954) claimed that magnesium and manganese were positively correlated with one another. It is possible that the effects of the interrelationship of magnesium and manganese may be of considerable importance in the cultivation of *Hevea brasiliensis* in Malaya where the strongly acidic nature of the soils may well be conducive to the production of both magnesium deficiency and manganese toxicity effects (MULDER and GERRETSEN 1952).

The total dry weight of the plant showed distinct variations with treatment. The response to increased potassium supply was an overall decrease in dry weight but the response to magnesium and phosphate addition changed with time. These changes, which may need subsequent confirmation, were correlated with corresponding changes in the vigour of the plants and suggested that during the early stages growth was limited by the magnesium supply whereas, later, development became more dependent on an increased supply of phosphate. These effects may possibly have been contributed to by the fact that the proportion of magnesium translocated from the seed to the seedlings was less than that of potassium and phosphorus. A similar change in effect of magnesium and phosphate levels was also noted for the concentration of rubber in the stems and petioles.

The lack of consistency from month to month in the effects of nutrient level on rubber concentration was noteworthy. Frequently these effects were significant but the net increase in the concentration value was never large (not more than 25%). The relatively small magnitude of the differences obtained suggested that the concentration of rubber within the plant was not directly affected by the nutrient concentration but only the total amount produced per plant; this is substantially the same inference as

was drawn from a previous entirely independent investigation (BOLLE-JONES 1954b). This does not preclude the possibility of much larger differences being obtained if the analysis could be carried out on rubber bearing tissues only.

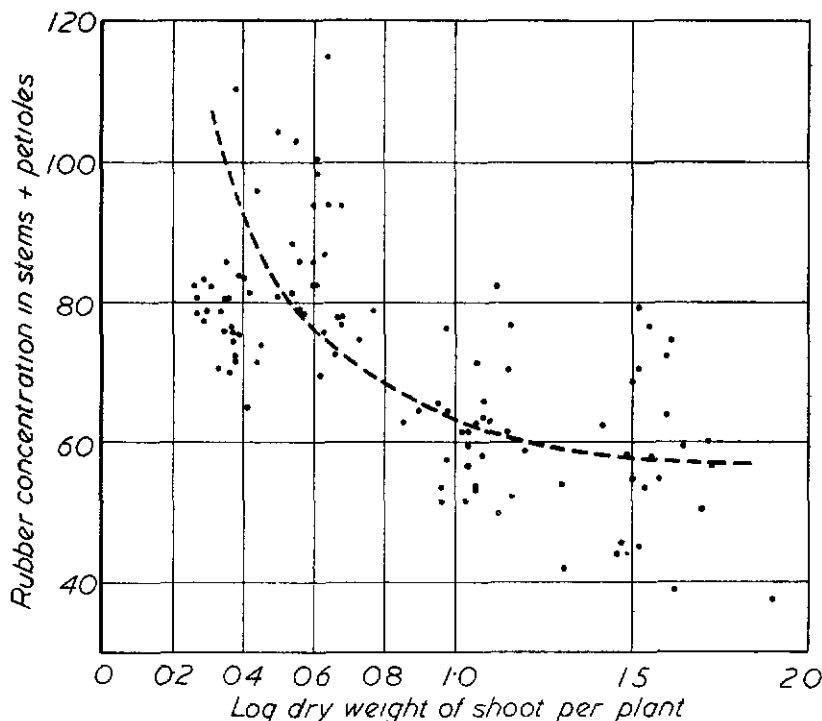


Figure 5. Decline in concentration of rubber in bulked stems and petioles with increasing dry weight of shoot per plant. Rubber concentration expressed as mg per 5 gm of tissue; dry weight given as logarithm of dry weight in grams. Each point represents mean of two replicates. Data based on samplings taken April, May, June and October.

The gradual decrease in concentration of rubber with increasing age of the plant was probably due to the increasing proportion of tissues not bearing rubber. Thus the dry weight of the shoot appeared to be inversely related to the concentration of rubber (Figure 5). Where only the 'green' part of the stems was bulked with the petioles for analysis (TABLE II, July) the concentration of rubber was appreciably higher than where no such differentiation between green and brown stem was made (June).

The visual observation that increased phosphate supply accentuated the severity of magnesium deficiency symptoms at the  $Mg_1$  level was not confirmed by a resultant lower magnesium concentration in the laminae. The K/Mg ratio values however showed marked increases in the laminae of the  $Mg_1K_3$  plants

due to increased phosphate supply (TABLE VIII) ; this trend which was most marked in the older whorls was also obvious in the second whorl of the  $Mg_1K_2$  plants. High K/Mg ratio values were found where magnesium deficiency symptoms were obvious. In general these ratio values seemed to furnish a better guide than the concentration of magnesium to the occurrence of magnesium deficiency symptoms.

TABLE VIII: VARIATION OF K/Mg RATIO IN LAMINA WITH P LEVEL IN THE  $Mg_1$  PLANTS

		Level	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
<i>Top whorl — means of July and October values</i>		P <sub>1</sub>	10	16	19	15
		P <sub>2</sub>	10	14	23	16
		P <sub>3</sub>	11	17	30	20
		Mean	10	16	24	17
		Level	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	Mean
<i>Second whorl — means of June and October values</i>		P <sub>1</sub>	14	38	120	57
		P <sub>2</sub>	18	43	157	73
		P <sub>3</sub>	19	59	164	81
		Mean	17	46	147	70

The differential effect of increased phosphate supply on magnesium nutrition according to the level of magnesium supply (which resulted in a higher magnesium concentration at the higher Mg levels and increased severity of magnesium deficiency symptoms at the  $Mg_1$  level) may explain why some authors have stated that added phosphate increased the magnesium content while others reported that it produced magnesium deficiency (*loc. cit.*). It is probable that in such studies the effect of phosphate on K/Mg ratio values (and not on magnesium concentration) would have yielded a better interpretation of the effects observed.

The practical significance of the results which have emerged from this investigation may be summarized as follows:

- (a) Heavy applications of phosphate in regions known to bear plants with magnesium deficient foliage may accentuate the severity of the deficiency. This supposition is independently supported by MULDER'S

- (1952) investigations on the nutrition of fruit trees from which he concluded that to increase the phosphorus content of apple leaves in magnesium deficient areas it was more economical to apply magnesium-containing rather than phosphorus-containing fertilisers.
- (b) The potassium requirement of *Hevea brasiliensis* may be low, as comparatively small concentrations of potassium in the nutrient frequently decreased the dry weight of the plant; a similar low requirement for potassium and the latter's adverse effect on girth increment has been noted in the annual report of the Soils Division for 1951. Hence routine applications of potassium to *Hevea* crops should be in small amounts and only when necessary. The incidence of potassium deficiency symptoms in Malaya has not yet been demonstrated.
- (c) For diagnostic and advisory purposes it is better, when examining leaves suspected of being incipiently deficient in magnesium, to evaluate and compare the K/Mg ratio values with those of healthy laminae rather than to depend solely on the concentration of magnesium as the decisive criterion.

It is recognised that the above points are based entirely on investigations carried out on young seedlings but until there is evidence to show that mature trees may react differently it would appear wiser to adhere to those recommendations.

#### SUMMARY

*Hevea brasiliensis* seedlings, clone Tjirandji 1, were grown in pot sand culture in a  $3^3$  factorial experiment in which magnesium, potassium and phosphate were each applied at deficiency, sufficiency and luxury levels of consumption.

In the earlier stages growth appeared to be more dependent on an adequate supply of magnesium than on phosphate; later this effect was reversed. Most of the effects on dry weight of plant, rubber and chlorophyll contents of the laminae were explicable on this basis.

The variation with nutrient level of the rubber concentration in bulked stem and petiole tissues was small, but potassium or phosphate addition gave positive and magnesium gave negative responses during early growth. These effects were inversely related to the dry weight trends and suggested a 'dilution' effect of non rubber bearing tissue on the rubber concentration values obtained.

Low magnesium supply or excessive amounts of potassium or phosphate (at the lowest magnesium level) produced severe magnesium deficiency symptoms which were associated with an elevated K/Mg ratio.

Evidence in support of a direct interrelationship between magnesium and phosphorus was presented: the levels of magnesium and phosphate supplied influenced the concentration of phosphorus and magnesium respectively in the lamina. The con-



centration of magnesium in the lamina was governed by the relative levels of magnesium and potassium and of magnesium and phosphate supplied to the plant while the concentration of phosphorus was determined by the relative levels of magnesium and phosphate.

An indirect relationship of magnesium and phosphate was reflected in their respective effects, usually opposite, on the chlorophyll and potassium concentrations in the lamina.

The close interrelationship of the three nutrients examined was illustrated in their effect on manganese concentration: increased magnesium level decreased while increased potassium or phosphate level increased the manganese concentration in the lamina. Attention was drawn to points of practical significance arising from the results.

*I am indebted to Mr D.K. Dutta Ray for the numerous statistical computations which this investigation necessitated.*

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Rubber Research Institute of Malaya  
Kuala Lumpur

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