2. The effect of nitrogen and phosphorus on the levels of two enzymes, pectase and protease, was also determined on the same material.

3. Phosphorus increases the non-protein, or carbohydrate, components of the leaf, while nitrogen increases the protein components.

4. Nitrogen increases pectase levels, while phosphorus decreases them. The reverse is true for protease. It is suggested that this may indicate the presence of different paths for the synthesis and breakdown of both pectin and protein.

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The Effect of Infection with Tobacco-Mosaic Virus on the Levels of Nitrogen, Phosphorus, Protease, and Pectase in Tobacco Leaves and on their Response to Fertilizers

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The effect of fertilizers on the levels of nitrogen, phosphorus, protease and pectase in healthy tobacco leaves has been described in a previous paper (Holden & Tracey, 1948). The plants used in getting the data given in this paper were a precisely similar series, but were infected with tobacco-mosaic virus.

Bawden (1943) and Wynd (1943) have reviewed the effects of virus infection on the metabolism of plants, and references to earlier work on tobacco infected with tobacco-mosaic virus can be found in their papers. The analyses described were made on tobacco plants supplied by Mr F. C. Bawden and Mr B. Kassanis, who were studying the effects of various fertilizer treatments on the susceptibility to infection and the multiplication of tobacco-mosaic virus. The data presented are restricted to a comparison of the nitrogen, phosphorus, protease and pectase levels in infected and healthy plants with different fertilizer treatments and the response to these treatments.

METHODS

Plants used. Tobacco (*Nicotiana tabacum* var. White Burley) plants were grown in pots in a heated glasshouse. The fertilizer treatments and levels were as described in the previous paper (Holden & Tracey, 1948).

Infection of the plants with tobacco-mosaic virus. In three experiments the plants were infected by rubbing five leaves with a virus preparation. These plants were harvested after 10–14 days, by which time only local virus multiplication had occurred. In the other two experiments the plants were infected when much younger, and grown for a period sufficient for the virus to spread systemically throughout the plant. The cultural history of the plants is given in Table 1.

Fractionation and analyses. The preparation of leaf fractions and their analysis has been described in the previous paper. pH determinations were made on spun sap using a glass electrode. Estimations of virus concentration were made on spun sap and washed fibre by Bawden & Kassanis (unpublished).

Analysis of data. The initial stages of the statistical analysis of the data were as described previously, except that the results from local and systemic infection were kept separate. The results for healthy controls were also analyzed, after these had been separated into groups corresponding to controls for local and systemic infection to eliminate seasonal differences. Standard errors for the means, and for the differences between means of healthy and infected plants, were calculated for both groups (systemic and local with their corresponding controls). A pooled standard error for the difference between fertilizer effects is given, as the individual standard errors were very similar.

Table 1. *Cultural history of the tobacco plants*

Date potted	Date of infection	Length of infection (days)	Average weight of plant* with full fertilizer supplement (g.)	Method of sampling (leaves taken)
11. x. 46	17. xii. 46	14	*I* 33·3 *H* 34·1	5
31. x. 45	12. ii. 46	10	*I* 106·0 *H* 92·0	5
4. ii. 46	17. iv. 46	10	*I* 52·6 *H* 105·2	5
21. v. 46	11. vi. 46	30	*I* 112·2 *H* 144·5	All
31. vii. 46	20. viii. 46	35	*I* 72·4 *H* 88·0	All

* Here and in later tables, *I* = infected; *H* = healthy.

RESULTS

The results obtained are given in Tables 2–6. In Table 3 relating to N, the N contents have been given both in terms of the total N, and also total N with virus N subtracted for the systemic experiments. Virus N figures were calculated from estimated amounts of virus on the assumption that its N content was 16·5 %.

The effects of systemic infection are summarized in Table 7.

The sap pH values are not recorded as there were no consistent differences either with different fertilizer treatments or with virus infection.

Table 2. *Dry matter content of tobacco plants*

Character determined	Condition of plant*	Extreme range	Mean	Standard error of difference between means of *I* and *H*†	Mean of untreated group	Mean of N, P and K group	Fertilizer effects: N	P	K	N and P	Standard error of difference between fertilizer effects on *I* and *H*†
Wet weight of plants (g.)	*L*	22–424	137	±16·1	75	285	+ 30	+150	+14	+ 55	±32·3
	H	35–526	162		75	355	+ 54	+162	+40	+ 51	
	S	20–561	192	±19·6	78	462	+137	+188	+46	+109	±39·4
	H	62–722	269		136	581	+164	+220	+26	+133	
Wet weight of leaves (g.)	*L*	14–262	78	± 7·4	51	148	+ 18	+ 64	+ 4	+ 29	±14·7
	H	22–268	79		51	147	+ 21	+ 57	+14	+ 22	
	S	17–412	156	± 8·9	70	348	+ 99	+134	+33	+ 72	±16·4
	H	56–451	208		120	386	+101	+124	+14	+ 73	
Dry matter (% of wet weight)	*L*	7·3–16·9	11·5	± 0·35	11·1	11·9	− 0·65	+ 0·70	+0·22	− 0·05	± 0·71
	H	7·1–16·8	11·1		10·6	11·8	− 0·57	+ 0·77	+0·43	+ 0·25	
	S	9·6–13·9	11·7	± 0·42	10·9	11·6	− 0·31	+ 1·59	−0·11	− 0·59	± 0·85
	H	10·0–16·1	13·1		13·3	12·8	− 1·43	+ 2·13	−0·48	+ 0·13	
Total dry matter (g.)	*L*	1·5–43·9	9·8	± 1·81	5·9	20·6	+ 2·8	+ 8·9	+0·9	+ 4·4	± 3·63
	H	1·8–44·9	9·8		5·6	19·9	+ 3·2	+ 8·0	+2·1	+ 3·3	
	S	1·8–51·9	18·5	± 2·21	8·0	40·4	+11·4	+17·3	+3·3	+ 8·3	± 4·42
	H	6·3–64·5	28·3		16·9	49·7	+11·1	+20·1	±0	+10·3	
Fibre dry matter (% total dry matter)	*L*	40–60	48·5	± 0·93	49	49	− 1·5	+ 2·0	−0·5	− 1·0	± 1·87
	H	42–57	49·5		47	48	− 3·0	+ 3·5	−1·0	± 0	
	S	45–66	55·3	± 1·13	50	54	− 5·0	+ 9·0	+1·0	− 2·0	± 2·26
	H	45–65	53·0		54	56	− 4·0	+ 8·0	−1·0	± 0	

* Here and in later tables, *L* = locally infected; *S* = systemically infected.
† See Table 1, footnote.

Table 3. *Nitrogen content of tobacco plants*

Character measured	Condition of plant*	Extreme range	Mean	Standard error of difference between means of *I* and *H*†	Mean of untreated group	Mean of N, P and K group	Fertilizer effects N	P	K	N and P	Standard error of difference between fertilizer effects on *I* and *H*†
N (% of dry matter)	*L*	1·10–5·80	3·32	±0·16	2·88	3·47	+1·84	− 0·49	−0·36	+0·05	±0·31
	H	1·03–5·65	3·29		3·06	3·43	+1·61	− 0·53	−0·50	+0·12	
	S	2·29–6·20	4·19	±0·20	3·85	4·74	+2·02	− 1·06	−0·13	+0·18	±0·40
	H	1·27–6·89	3·19		2·52	2·91	+2·33	− 1·57	−0·14	−0·72	
Total N (mg.)	*L*	83–763	259	±59	158	499	+172	+182	− 27	+132	±117
	H	75–691	258		161	447	+171	+120	±0	+ 87	
	S	111–2050	765	±72	290	1823	+792	+619	+120	+477	±144
	H	231–3282	805		370	984	+807	+327	−113	+282	
Sap N (% of dry matter)	*L*	2·10–8·80	4·53	±0·21	3·64	4·70	+2·52	− 0·76	−0·31	−0·40	±0·41
	H	2·17–6·90	4·49		3·90	4·70	+2·41	− 1·26	−0·25	−0·50	
	S	3·15–8·95	5·30	±0·25	4·52	4·80	+2·43	− 1·54	−0·58	−0·71	±0·50
	H	1·84–9·23	4·28		3·13	3·61	+3·19	− 2·12	−0·41	−1·45	
Sap N (mg./ml.)	*L*	1·18–3·91	2·20	±0·11	1·83	2·36	+1·22	− 0·52	−0·13	−0·26	±0·23
	H	1·04–4·47	2·16		1·93	2·37	+1·15	− 0·62	−0·22	−0·14	
	S	1·48–4·24	2·82	±0·14	2·34	2·79	+1·62	− 0·79	−0·21	−0·11	±0·28
	H	1·16–4·52	2·27		1·72	2·01	+1·82	− 1·10	−0·24	−0·63	
Sap protein N (mg./ml.)	*L*	0·71–2·34	1·37	±0·08	1·24	1·75	+0·52	+ 0·03	−0·01	+0·13	±0·16
	H	0·61–2·62	1·28		1·16	1·74	+0·54	+ 0·04	−0·02	+0·18	
	S	1·11–2·80	1·84		1·57	2·20	+0·89	± 0	−0·10	+0·31	
	S	(0·57–2·26	1·30	±0·10	1·10	1·46	+0·81	− 0·26	−0·05	+0·16)	±0·20
	H	0·47–1·78	1·08		0·87	1·29	+0·77	− 0·17	−0·08	+0·14	
Sap sediment N (% of non-fibre N)	*L*	10·4–22·2	16·3	±1·1	16·9	16·4	−0·1	− 0·1	−1·1	+2·4	±2·3
	H	10·0–24·3	16·6		14·7	15·1	−1·4	+ 1·7	−1·1	+1·3	
	S	12·4–23·0	16·8	±1·4	18·8	13·9	−2·7	− 1·7	−1·2	+0·7	±2·8
	H	9·9–30·3	19·9		20·3	15·4	−5·4	− 1·7	+0·4	+0·6	
Fibre N (% of dry matter)	*L*	0·75–4·98	2·78	±0·15	2·64	2·92	+1·23	− 0·18	−0·47	+0·23	±0·31
	H	0·74–5·08	2·67		2·54	2·79	+1·07	− 0·07	−0·53	+0·37	
	S	2·07–4·90	3·53		3·51	3·86	+1·40	− 0·69	−0·16	+0·47	
	S	(0·51–3·77	2·41	±0·19	2·69	2·11	+1·14	− 1·37	−0·10	+0·19)	±0·37
	H	1·07–5·65	2·62		2·22	2·76	+1·77	− 0·82	−0·06	−0·14	
Fibre N (% total N)	*L*	34–48	41·2	±1·26	45	41	−5·1	+ 4·3	−3·4	+2·4	±2·5
	H	27–50	38·8		39	39	−2·8	+ 6·2	−1·8	+2·2	
	S	35–57	45·6	±1·56	44	56	−1·1	+10·3	+0·1	+6·4	±3·1
	H	29–59	47·2		48	54	−5·4	+13·9	+0·4	+5·1	

* See Table 2, footnote.

† See Table 1, footnote.

DISCUSSION

The data given in tabular form offer opportunities for extended discussion and speculation. It is proposed, however, to restrict the scope of the discussion, but increase its validity, by considering only differences in means of values for infected and healthy plants, and by excluding any that are not at least twice as great as the calculated standard error for differences between means.

Local multiplication of the virus for a period of about 10 days results in no significant change in the response of the plants to fertilizer supplements, and to a difference in composition between healthy and infected plants only in the percentage of total P that is in fibre.

Continued multiplication of the virus with its spread throughout the leaves has some effect on the response to fertilizer treatment, and causes profound changes in the size and composition of the leaves. There are four instances of significant changes in fertilizer response. The positive effect of P supplements on the total N of the leaves is increased and the K effect is reversed. The negative effect of N and the positive effect of P on the protease units/g. protein N of sap are both significantly enhanced. In

Table 4. *Phosphorus content of tobacco plants*

Character measured	Condition of plant*	Extreme range	Mean	Standard error of difference between means of *I* and *H*†	Mean of untreated group	Mean of N, P and K group	Fertilizer effects N	P	K	N and P	Standard error of difference between fertilizer effects on *I* and *H*†
P (% of dry matter)	*L*	0·096–0·593	0·256	±0·020	0·131	0·244	+ 0·016	+ 0·175	−0·032	− 0·022	±0·040
	H	0·092–0·455	0·238		0·198	0·472	− 0·003	+ 0·216	−0·021	− 0·008	
	S	0·182–0·600	0·318	±0·024	0·214	0·428	+ 0·030	+ 0·210	−0·080	− 0·046	±0·048
	H	0·142–0·470	0·247		0·155	0·330	+ 0·030	+ 0·170	−0·040	− 0·016	
Total P (mg.)	*L*	5·32–66·35	25·20	±2·1	5·51	35·84	+ 7·73	+31·03	−2·20	+ 8·21	±4·3
	H	2·51–36·46	24·20		6·70	43·81	+ 3·84	+28·80	+2·94	+ 4·06	
	S	4·30–165·4	65·50	±2·7	17·00	158·60	+50·84	+90·11	+1·64	+46·75	±5·4
	H	10·10–187·2	75·40		25·26	157·00	+42·24	+95·01	−9·05	+38·95	
Sap P (% of dry matter)	*L*	0·10–0·59	0·357	±0·054	0·100	0·230	− 0·043	+ 0·236	−0·010	− 0·070	±0·108
	H	0·09–0·78	0·295		0·130	0·430	− 0·038	+ 0·330	−0·033	− 0·034	
	S	0·16–0·89	0·432	±0·066	0·220	0·550	− 0·070	+ 0·430	−0·050	− 0·050	±0·133
	H	0·14–0·72	0·448		0·180	0·540	+ 0·066	+ 0·529	−0·189	+ 0·054	
Fibre P (% of dry matter)	*L*	0·080–0·380	0·200	±0·013	0·130	0·221	+ 0·040	+ 0·100	−0·050	− 0·010	±0·026
	H	0·080–0·400	0·183		0·120	0·220	+ 0·029	+ 0·128	−0·046	+ 0·018	
	S	0·185–0·395	0·250	±0·016	0·200	0·322	+ 0·061	+ 0·070	−0·018	+ 0·061	±0·031
	H	0·140–0·390	0·198		0·160	0·241	+ 0·051	+ 0·089	−0·039	− 0·039	
Fibre P (% total P)	*L*	32–56	42·5	±1·4	45·0	39·5	+ 0·3	− 0·6	+0·4	− 0·3	±2·8
	H	26–55	39·6		43·6	36·3	+ 1·6	− 4·6	−0·9	+ 6·1	
	S	27–56	44·3	±1·8	47·0	40·5	+ 3·6	−10·0	−1·1	+ 2·0	±3·5
	H	29–63	45·9		54·5	43·0	+ 4·0	− 7·8	−5·5	+ 3·3	

* See Table 2, footnote.

† See Table 1, footnote.

general, however, it may be said that the response to fertilizers of infected plants is similar to that shown by healthy plants.

Infection in the early stages of growth, leading to systemic spread of virus is well known to result in a yellowing of the leaves and a stunting of the plant. This stunting is shown in Table 2 as a reduction in the wet weight of the leaves, and there is a greater proportionate reduction of total dry matter, resulting in a wetter leaf. The decrease in dry matter is accompanied by a decrease in the total P, but the decrease in P content is less than that of dry matter so there is an increase in the P as percentage of total dry matter, and as percentage of dry matter of the fibre fraction. The increase is greater than can be accounted for by virus P.

During the yellowing of the leaves in tobacco-mosaic infection there may be a reduction in the chlorophyll content by as much as 60 % (Peterson & McKinney, 1938). The reduction in chlorophyll is presumably accompanied by a decrease in the amount of protein with which it is associated. Woods & Du Buy (1941) have shown that, particularly under conditions of N starvation, chromoprotein diminishes in leaves as the amount of virus increases. In the present experiments there was a significant decrease in infected leaves in the sap-sediment N fraction, which contains much of the chromoprotein. As the leaves taken from infected plants were in various physiological states, from small dark green and large yellow green to completely yellow leaves, the difference is not as great as would be expected if yellow leaves only from infected plants were compared with leaves of the same age from healthy plants.

The reduction in the carbohydrate content of tobacco leaves infected with tobacco-mosaic virus found by Dunlap (1930, 1931) agrees with the findings reported here, for, while there is a decrease in the total dry matter, there is no decrease in total N. Dunlap found that there was a greater decrease in the starch and sugar content than in that of the other carbohydrates. This would be in agreement with the present findings that there was a greater loss of soluble fractions, which resulted in a greater proportion of the dry matter being in the fibre. Cordingley, Grainger, Pearsall & Wright (1934) also found a decrease in total carbohydrate, but found that the proportion of the various fractions was the same in infected and healthy plants. These different results may be due to the different methods of fractionation and estimation used.

As systemic infection has no significant effect on the total N of the leaves it leads to an increase in N as percentage of dry matter. The distribution of N between fibre and soluble fractions is not altered,

Table 5. *Protease content of tobacco plants*

Character measured	Condition of plant*	Extreme range	Mean	Standard error of difference between means of *I* and *H*†	Mean of untreated group	Mean of N, P and K group	Fertilizer effects: N	P	K	N and P	Standard error of difference between fertilizer effects on *I* and *H*†
Total protease (units/g. dry weight)	*L*	1·4–10·5	4·2	± 0·34	3·7	5·0	−0·7	+1·3	−0·2	−0·4	± 0·68
	H	2·0– 8·9	4·2		3·3	4·9	−0·5	+1·4	+0·4	+0·1	
	S	1·4–7·1	3·3	± 0·42	2·6	4·5	+0·4	+1·5	+0·2	+0·6	± 0·85
	H	0·6–4·1	2·7		2·2	3·8	±0·0	+0·7	+0·3	+0·6	
Protease (units/g. protein N)	*L*	48–545	186	±20	185	148	−70	+18	−49	−58	±40
	H	35–428	183		136	184	−91	+74	+24	−26	
	S	36–225	101	±24	110	154	−43	+56	+15	−18	±48
	H	20–203	117		78	100	−55	+41	±0·0	+25	
Protease (units/ml. sap)	*L*	0·04–0·60	0·34	± 0·031	0·29	0·46	−0·13	+0·15	−0·01	+0·04	± 0·062
	H	0·07–0·63	0·34		0·25	0·39	−0·13	+0·08	+0·08	−0·04	
	S	0·07–0·42	0·22	± 0·038	0·17	0·26	−0·01	+0·10	+0·02	+0·01	± 0·077
	H	0·03–0·49	0·25		0·19	0·33	−0·05	+0·12	+0·03	+0·02	
Protease (units/g. dry weight sap)	*L*	1·0–15·0	7·1	± 0·62	5·6	9·2	−2·6	+3·4	−0·4	+0·5	± 1·25
	H	1·5–13·3	7·1		5·0	7·5	−3·3	+1·4	+2·4	−1·3	
	S	1·2– 8·8	4·3	± 0·76	6·7	3·0	−0·9	+2·0	+0·4	−0·5	± 1·53
	H	0·5–10·5	4·9		3·7	0·7	−1·5	+2·4	+0·5	−0·1	
Protease (units/g. protein N of sap)	*L*	36–792	290	±39·9	236	293	−230	+154	−16	− 37	±80·0
	H	38–892	316		213	251	−248	+140	+90	−125	
	S	27–350	141	±48·6	112	127	−78	+ 67	+23	− 41	±97·2
	H	25–1040	300		204	261	−279	+224	+78	−126	
Protease (units/g. dry weight of fibre)	*L*	1·0–11·7	3·7	± 0·38	3·4	5·1	+0·4	+0·7	+0·6	+0·6	± 0·77
	H	1·4–12·4	3·4		2·7	4·9	+0·9	+1·7	−0·3	+0·7	
	S	1·7–8·8	3·4	± 0·47	2·5	4·2	+1·0	+1·3	−0·7	+0·9	± 0·94
	H	1·2–3·8	2·4		1·8	3·6	+0·6	+0·2	+0·4	+0·7	
Fibre (units/g. N)	*L*	21–284	128	± 8·6	121	149	−44	+37	+27	− 6	±17·3
	H	22–262	132		107	159	−34	+73	+ 9	−12	
	S	35–196	93	±10·6	68	105	−16	+55	− 9	+ 1	±21·2
	H	26–150	98		85	126	−43	+33	+23	+20	

* See Table 2, footnote.

† See Table 1, footnote.

Table 6. *Pectase content of tobacco plants*

Character measured	Condition of plant*	Extreme range	Mean	Standard error of difference between means of *I* and *H*†	Mean of untreated group	Mean of N, P and K group	Fertilizer effects: N	P	K	N and P	Standard error of difference between fertilizer effects on *I* and *H*†
Fibre (units‡/g. dry matter)	*L*	0·10–0·61	0·29	±0·050	0·35	0·24	+0·125	− 0·234	−0·013	−0·026	±0·10
	H	0·07–0·51	0·26		0·34	0·20	+0·106	− 0·216	−0·009	−0·028	
	S	0·08–0·95	0·46		0·55	0·41	+0·194	− 0·340	+0·081	−0·038	
	H	0·08–1·31	0·42		0·46	0·25	+0·225	− 0·482	±0	−0·103	
Fibre (units/g. N)	*L*	4·35–22·20	11·60	±1·50	15·30	11·28	−1·37	− 6·50	+2·16	+2·90	±3·00
	H	4·45–17·20	9·81		13·01	9·07	−0·16	− 5·32	+1·68	+0·72	
	S	3·78–24·10	12·33		15·50	10·61	+1·62	− 7·37	−0·72	+2·16	
	H	6·70–33·45	15·58		21·92	7·65	−2·25	−14·65	+0·69	+0·69	

* See Table 2, footnote.

† See Table 1, footnote.

‡ For definition of units see Holden (1946).

and there is a corresponding increase in N as percentage of dry matter of both sap and fibre fractions. One of the results of infection is an increase in the rate at which the leaves yellow, which leaves of healthy plants do with increased age. The yellow healthy leaves, like the infected leaves, have a higher water content than healthy green leaves (Smirnow, 1940), but, unlike infected leaves, have less N/100 g. dry matter. If virus N is subtracted from the total N the infected leaves still do not have less N/100 g. dry matter, so infection cannot be regarded simply as a premature ageing of the leaves.

Table 7. *Effects of systemic infection of tobacco plants*

Decrease in:	Wet weight of plants
	Wet weight of leaves
	Total dry matter
	Total phosphorus
	Dry matter as % wet weight
	Sap sediment N as % non-fibre N
	Protease/g. protein N of sap
	Pectase/g. N of fibre
Increase in:	Total N as % dry matter
	Fibre N as % dry matter
	Sap N as % dry matter
	Total P as % dry matter
	Fibre P as % dry matter
	Sap N/ml.
	Protein N/ml.
	% total dry matter as fibre
	Total protease/g. dry weight
	Fibre protease/g. dry weight
No significant change in:	Total N
	% total N on fibre
	% total P on fibre
	Sap P as % dry matter
	Total units protease/g. total protein N
	Fibre protease/g. N
	Pectase/g. dry matter of fibre

Considering the mean of all treatments, about one third of the total N is virus N, in agreement with Bawden & Pirie (1946). But the range is from 10 to 65 % of the total N as virus N, and in one experiment (with plants given P but no N) 80 % of the fibre N was virus N. It is certain that the protein components of systemically infected leaves are affected differently, as, for example, the decrease in chromoprotein mentioned earlier. Several authors have referred to changes in enzyme levels caused by virus infection (Balls & Martin, 1938; Peterson & McKinney, 1938; Wynd, 1942). In the present experiments systemic infection affected protease and pectase levels differently. Fibre pectase was related to non-virus N, while fibre protease was related to total N levels. Sap protease, on the other hand, was related to non-virus protein rather than to total protein N.

SUMMARY

1. The effects of supplements of nitrogen and phosphorus on the nitrogen and phosphorus content of leaf fractions of tobacco plants with local and systemic multiplication of tobacco-mosaic virus were similar to those found with healthy plants.

2. The effect of local multiplication of tobacco-mosaic virus on the composition of the leaf fractions studied was negligible.

3. The effect of systemic multiplication of tobacco-mosaic virus on the composition of the fractions studied was profound.

4. Total nitrogen was not affected, while dry matter and phosphorus were reduced.

5. The levels of the two enzymes studied were affected differently. Fibre protease was related to total fibre nitrogen while pectase appeared to be related to non-virus fibre nitrogen.

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