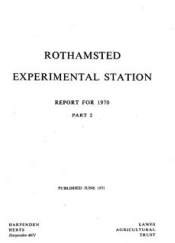
Rothamsted Experimental Station Report for 1970 Part 2



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ROTHAMSTED

EXPERIMENTAL STATION

REPORT FOR 1970

PART 2

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Relationships Between the Composition of Soils and Physical Measurements made on them

R. J. B. WILLIAMS

The good drainage and aeration of soils that is essential for roots to grow satisfactorily can be ensured only by enough pores of the right sizes together with cracks and fissures leading through the soil and subsoil. Pore space is lost when aggregates are 'slaked', either by water or mechanically when soil is compressed or deformed. In the work described in this paper the stability and strength of the aggregates in 189 soils were measured, and measurements related to each other and to the compositions of the soils. The laboratory tests simulated some of the conditions in field soils, created either by weather or cultivations. They involved two physical processes, disintegration (slaking) and cohesion. Slaking can be caused by the capillary action of water, or by mechanical pressure on dry soil, or by both. Cohesion expresses the resistance of aggregates to mechanical forces that might break them—important in assessing the effects of implements intended to make soil finer.

The soils were mainly from arable land in Great Britain, wherever possible from sites of field experiments about which there was already some other information. Thirty-seven soils were from Woburn and 27 from Rothamsted; the other British soils came from the following counties: Bedford, Buckingham, Cambridge, Cardigan, Cheshire, Cornwall, Derby, Dorset, Essex, Gloucestershire, Hampshire, Hereford, Hertford, Huntingdon, Kent, Lancashire, Leicester, Lincoln, Norfolk, Northampton, Nottingham, Shropshire, and Suffolk. There were also 13 soils from Ireland.

The soils were prepared (as air-dry aggregates) in a standard way to obtain comparable results; the tests were made with simple and easily constructed apparatus. Table 1 shows groupings of soils. More than half were arable topsoils. A sixth were rich in organic matter because of organic manuring; a sixth were grassland soils and a few were from woodland and subsoils. Nearly three-quarters of the soils had less than 2% organic carbon—representative of much arable land in England.

TABLE 1

Description of soil used

History	Number of soils	Major groups	Percentage
Fallows	9		
Subsoils	10	118	62
Arable topsoils	99		
Arable (sewage sludge or compost treated)	17		
Arable (receiving farmyard manure)	14	34	18
Woodland	3		
Grassland (ploughed)	17		
Grassland (under ley)	5	37	20
Grassland (permanent pasture)	15		
Soils >2·00% organic carbon	49	—	—
Soils <2·00% organic carbon	140	—	—

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Methods

The physical methods used were described by Williams and Cooke (1961). A portion of each soil was air-dried and a fraction passing a 2 mm sieve was used to measure bulk density, water-holding capacity and mechanical composition, and for chemical analyses. The remainder was used to prepare aggregates for the tests by freezing, thawing and air-drying. It was wetted until moist, but not sticky, packed into polythene tubing and maintained at −15°C for three days. The sample was removed from the tube, allowed to thaw, dry and disintegrate; drying at room temperature was assisted by a fan. Aggregates with diameters in the range 4–6 mm were separated by round-holed sieves, using no force, and were stored so that they could not be mechanically damaged.

Bulk density (BD). British Standards Institution (1948) method.

Water-holding capacity (WHC). 20 g soil (<2 mm) were saturated with water for several hours; the water remaining after draining overnight was measured.

pH. pH was measured in a 1 : 2·5 suspension by glass electrode.

Water-slaking (I/WS). The percentage change in volume of a column of 30 g of 4–6 mm aggregates when wetted from below was measured (Williams & Cooke, 1961). Changes in the soils during slaking were observed with a hand lens.

Dry (mechanical) slaking (I/DS). 100 g of 4–6 mm aggregates in a column were compressed at 7·03 kg/cm² for 1 minute; percentage loss in volume was measured.

Total mechanical slaking (I/MS). The two tests were combined by compressing soil already slaked by water. (The pressure used, 7 kg/cm², caused about half as much compaction as pressure six times as large.)

Breaking strength (BS). The load needed to split a section (25 mm long and 25 mm diameter) of the compressed and air-dried cylinder produced by the previous mechanical slakings was measured. A polished steel penetrometer, 12·5 mm diameter with a hemispherical tip, was used and the section from the soil cylinder that was closest to the plunger when it was formed by mechanical slaking was chosen.

Mechanical composition. The gravel and coarse organic debris in the soil used for the water-slaking test were separated by elutriation and sieving. Coarse sand (2·0–0·2 mm) and fine sand (0·20–0·02 mm) were separated by decanting and sieving after destroying organic matter by hydrogen peroxide.

A separate portion of the original sample was used to measure % silt (0·02–0·002 mm) and % clay (<0·002 mm).

Loss on ignition. Percentage loss on ignition of <2 mm soil heated at 800°C in a muffle furnace for 2 hours was measured.

Chemical measurements. Williams' (1948) manometric method was used to measure $\%CaCO_3$. %N was referred to <2 mm soil dried at 105°C, by a Kjeldahl method (Bremner, 1960) using Cu and Se as catalysts. Walkley and Black's method (Walkley,

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1935) was used on <0·5 mm soil to measure % organic carbon; the results given here are as determined.

Table 2 gives correlation coefficients between the physical and chemical measurements on the soils.

TABLE 2

Correlation coefficients between soil composition variates

	Coarse particles 6–0·02 mm	Coarse particles 6–0·2 mm	OC %	N %	COM %	Silt %	Clay %
			Arable soils (DF 145)				
% Coarse particles (CP) (6–0·02 mm)	1·00	—	—	—	—	—	—
% Coarse particles (6–0·2 mm)	0·85	1·00	—	—	—	—	—
% Organic carbon (OC)	−0·51	−0·35	1·00	—	—	—	—
% Total nitrogen (N)	−0·60	−0·43	0·92	1·00	—	—	—
% Coarse organic matter (COM) (2–6 mm)	−0·22	−0·17	0·41	0·39	1·00	—	—
% Silt (0·02–0·002 mm)	−0·73	−0·69	0·30	0·35	0·14	1·00	—
% Clay (< 0·002 mm)	−0·78	−0·62	0·35	0·42	0·13	0·17	1·00
			Grassland soils (DF 35)				
% Coarse particles (6–0·02 mm)	1·00	—	—	—	—	—	—
% Coarse particle (6–0·2 mm)	0·85	1·00	—	—	—	—	—
% Organic carbon	−0·58	−0·39	1·00	—	—	—	—
% Total nitrogen	−0·70	−0·42	0·92	1·00	—	—	—
% Coarse organic matter (2–6 mm)	−0·24	−0·21	0·40	0·37	1·00	—	—
% Silt (0·02–0·002 mm)	−0·84	−0·71	0·39	0·51	0·27	1·00	—
% Clay (< 0·002 mm)	−0·72	−0·69	0·05	0·24	−0·08	0·40	1·00

Results

Table 3 gives average values for each of the properties measured. Grassland soils slaked much less readily than arable soils in water but the two differed less in the dry slaking test. Test cylinders formed by compacting arable soils were much stronger than those from grassland. Arable soils had larger bulk densities, but held less water and contained less N and C than grassland soils. Differences of these kinds were expected.

The reproducibility of the tests employed was examined by making ten replicate measurements on seven soils chosen for widely different mechanical compositions and organic carbon contents. Table 4 gives average values and standard deviations. When soils were very stable to water (i.e. per cent loss in pore space on wetting was small), the value was not accurately determined. With values smaller than 5%, standard deviations tended to be of the same size. This was because stable soils were usually rich in organic carbon and clay, which made them swell without slaking and stick to the tube used in the test, obscuring movement of the column of soil. Larger instabilities were measured more accurately. The other properties were also measured quite accurately. Measuring the very small loss in pore space accurately for groups of very stable soils is not important, except when comparing the effects of experimental treatments that may alter physical properties. Where accurate measures are needed on stable soils an alternative, more sensitive, procedure described by Williams (1963) can be used.

Comparisons of individual soil properties

The soil properties considered most likely to alter the physical attributes measured were organic matter content and mechanical composition (especially the proportions of

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TABLE 3

Summary of results of physical tests and chemical analyses on 189 soils

Soil test or analysis	All soils (189)			Arable soils (147)			Grassland soils (37)		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum
% Water slaking instability (I/WS)	−3·4	20·2	60·1	−3·4	22·4	60·1	−2·1	7·7	42·0
% Dry slaking instability (I/DS)	8·6	21·6	48·5	8·6	21·6	44·9	10·9	19·8	37·3
% Total mechanical slaking (I/MS)	27·4	59·0	79·2	44·9	60·1	79·2	27·4	54·2	65·3
Breaking strength (kg) (BS)	0·12	5·99	17·00	0·12	6·10	17·00	1·05	4·49	14·75
Bulk density (<2 mm soil g/ml) (BD)	0·76	1·26	1·63	0·76	1·28	1·63	0·85	1·17	1·39
% Water holding capacity (<2 mm soil) (WHC)	12·8	49·4	99·3	12·8	47·1	85·4	29·4	60·0	99·3
Absolute density (g/ml)	2·17	2·51	2·75	2·25	2·53	2·75	2·17	2·46	2·63
pH in water	3·8	7·0	8·8	3·8	7·1	8·3	5·2	6·6	7·9
% Free calcium carbonate	0·0	3·9	82·8	0·0	3·7	82·8	0·0	2·2	61·6
% Organic carbon (Walkley & Black)	0·21	1·72	7·05	0·21	1·54	4·06	1·02	2·52	7·05
% Total nitrogen	0·04	0·20	0·68	0·04	0·18	0·42	0·11	0·27	0·68
% Coarse organic matter (2–6 mm) (COM)	0·0	0·11	1·01	0·00	0·08	0·69	0·01	0·21	1·01
% Coarse particles (6–0·02 mm) (CP)	11·9	59·8	91·8	11·9	61·4	91·8	22·5	54·1	84·9
% Coarse particles (6–0·2 mm)	0·1	31·2	84·1	0·1	33·2	84·1	4·3	25·5	72·1
% Silt (0·02–0·002 mm)	0·5	17·3	64·7	2·8	16·5	64·7	4·4	19·9	56·7
% Clay (<0·002 mm)	0·4	16·2	57·6	0·4	15·8	57·6	6·0	18·0	35·8

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TABLE 4

Reproducibility of soil physical test on different soils

		A	B	C	D	E	F	G
Soil composition	% Organic carbon	0·50	0·64	1·11	2·21	2·63	0·67	2·34
	% Coarse particles	48·0	79·0	81·8	56·0	39·8	82·0	54·6
	% Clay	29·3	10·3	8·0	22·3	23·7	9·7	22·5
Physical test								
% Water slaking instability		10·01 ±2·72	—	4·12 ±3·02	—	−1·74 ±1·23	36·50 ±2·34	—
% Dry slaking instability		6·71 ±0·66	15·50 ±1·19	17·36 ±0·79	7·86 ±0·44	—	—	—
% Total mechanical slaking		55·72 ±1·44	64·8 ±1·48	51·4 ±1·35	59·47 ±2·25	—	—	—
Breaking strength (kg)		9·97 ±0·72	5·28 ±0·66	1·45 ±0·19	8·07 ±1·53	—	—	—
Bulk density (< 2 mm soil) (g/ml)		1·274 ±0·008	1·454 ±0·014	—	—	—	—	—
% Water holding capacity (< 2 mm soil)		—	—	49·47 ±1·55	—	—	—	53·57 ±1·70

coarse particles of sand and gravel). These are examined in Tables 5 (gravel + coarse sand), 6 (gravel + coarse sand + fine sand) and 7 (organic carbon), where the soils are divided into groups of equal numbers (to provide comparable results) with increasing % organic C, or increasing % coarse particles. Correlation coefficients between each soil physical test and each soil property measured were calculated (Table 8), also linear regression coefficients (Table 9). In the following sections the effects of soil properties on each of the measurements made are discussed, individually from Tables 3, 5, 6, 7, 8 and 9 and from Figs. 1–5, which plot some detailed comparisons for bulk densities, the instability tests, and soil cylinder strengths.

Correlations between the results of the six tests on the soils are shown in Table 10 for arable and grassland soils separately. Instability to water was well correlated with instability to mechanical pressure by arable but not by grassland soils; as might be expected, there was some correlation between total instability to water and pressure combined, and to both water slaking and dry slaking tested separately. Breaking strength of cylinders was correlated with instability both in water and on dry slaking for arable soils, but only with dry slaking for grassland soils. Bulk density was correlated with amount of water slaking of arable soils and with wet slaking, total slaking, and breaking strengths of cylinders for grassland soils. Water-holding capacity (WHC) was well correlated with bulk density in grassland, but less closely in arable soils; WHC was correlated with results of all slaking tests on arable soils but was not closely related to dry mechanical slaking of grassland soils.

Bulk density (BD). The relationship between apparent density and absolute density shows total pore space in soils. Arable soils as a whole were more dense, and the range of values was greater, than grassland soils. Soils with more coarse particles tended to be more dense than finer textured soils (Fig. 1a) and relationships were clearer when the 'coarse' fraction included fine sand. The densities of groups of soils with more than 2% organic carbon differed considerably from those with less than 2% (Fig. 1b). The effects of organic carbon content were clear and consistent (Table 7, Fig. 1c and d), with bulk

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TABLE 5

Effects of increasing amounts of coarse mineral particles (6–0·2 mm) on soil properties

Range of particles 6–0·2 mm %	Number of soils	Particles 6–0·2 mm Mean %	Bulk density g/ml (< 2 mm soil)	Instability I/WS %	Instability I/DS %	Instability I/MS %	Breaking strength kg	Organic carbon %	Total nitrogen %	Absolute density g/ml
All soils										
0·1– 5·9	21	2·9	1·23	19·4	19·0	54·6	9·64	1·98	0·20	2·49
6·0–10·1	21	8·6	1·22	8·6	16·0	56·1	8·84	1·91	0·22	2·46
10·3–14·7	21	12·6	1·17	4·3	16·3	51·7	6·68	2·40	0·27	2·45
15·0–22·5	21	18·2	1·23	9·6	14·9	57·5	8·96	1·95	0·22	2·47
22·7–30·0	21	25·9	1·21	11·8	18·2	58·4	5·96	2·09	0·24	2·48
30·6–40·0	21	35·4	1·26	20·0	20·6	61·6	5·58	1·35	0·16	2·55
40·9–55·6	21	47·3	1·32	30·4	27·5	63·6	4·88	1·08	0·13	2·56
55·9–65·2	21	60·4	1·35	37·3	31·4	62·6	2·13	1·07	0·12	2·57
66·5–84·1	21	69·4	1·33	38·5	30·9	62·8	2·13	0·96	0·11	2·57
0·1–84·1	189	31·2	1·26	20·0	21·5	58·8	6·04	1·60	0·19	2·51
140 soils with < 2·00% organic carbon										
0·1– 8·5	20	3·4	1·24	22·0	19·6	56·6	9·90	1·28	0·16	2·52
8·7–14·7	20	10·9	1·30	10·9	15·9	57·1	9·37	1·35	0·17	2·51
15·2–27·0	20	20·6	1·24	11·5	15·7	59·1	8·11	1·38	0·17	2·52
28·0–38·8	20	33·6	1·31	23·8	20·3	62·7	6·32	1·19	0·14	2·55
39·3–55·6	20	47·4	1·33	34·2	28·8	64·3	4·97	0·93	0·11	2·57
55·9–65·5	20	60·5	1·35	37·2	30·6	63·2	2·29	0·91	0·11	2·58
66·0–84·1	20	69·6	1·33	38·5	30·7	62·6	2·17	0·99	0·11	2·57
0·1–84·1	140	35·1	1·30	25·4	23·1	60·8	6·16	1·14	0·14	2·54
49 soils with > 2·00% organic carbon										
2·1–12·4	16	7·8	1·11	0·7	17·6	49·3	6·94	3·22	0·35	2·37
12·7–23·3	16	16·7	1·14	2·6	15·1	52·4	6·16	3·04	0·33	2·41
23·6–63·8	17	34·4	1·18	9·4	21·3	56·8	4·29	2·50	0·27	2·46
2·1–63·8	49	19·9	1·14	4·3	18·1	52·9	5·76	2·91	0·31	2·41

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TABLE 6

Effects of increasing proportions of gravel, coarse and fine sand (6–0·02 mm) on soil properties

Range of particles 6–0·02 mm %	Number of soils	Particles 6–0·02 mm Mean %	Bulk density g/ml (< 2 mm soil)	Instability			Breaking strength kg	Organic carbon %	Total nitrogen %	Absolute density g/ml
				I/WS %	I/DS %	I/MS %				
All soils										
11·9–35·2	21	26·0	1·20	5·8	13·1	50·5	11·36	2·39	0·288	2·41
35·6–44·6	21	40·2	1·20	11·4	16·8	54·4	8·16	2·18	0·251	2·41
45·4–50·5	21	48·5	1·22	11·4	16·5	57·1	7·84	1·99	0·226	2·48
50·7–54·6	21	52·3	1·21	8·6	17·0	52·5	6·43	1·94	0·229	2·48
54·7–61·0	21	57·7	1·24	10·7	18·0	57·9	6·24	1·63	0·179	2·52
62·3–71·2	21	66·2	1·25	21·4	21·4	62·0	6·37	1·32	0·161	2·53
71·6–71·5	21	77·5	1·29	33·6	27·5	63·3	3·45	1·25	0·144	2·55
81·6–84·5	21	82·6	1·32	36·4	31·0	63·5	2·20	1·14	0·128	2·61
84·6–91·8	21	87·3	1·40	40·8	33·7	62·5	2·36	0·61	0·066	2·61
11·9–91·8	189	59·8	1·26	20·0	21·7	58·2	6·04	1·60	0·186	2·51
Soils with < 2·00% organic carbon										
22·3–44·6	20	35·1	1·28	16·1	16·6	55·6	11·29	1·32	0·170	2·50
47·4–51·8	20	49·8	1·28	14·3	15·2	59·2	9·33	1·40	0·176	2·52
52·2–60·9	20	56·9	1·27	13·1	17·2	59·3	6·99	1·27	0·149	2·54
62·3–71·2	20	66·3	1·27	22·0	21·4	62·0	6·47	1·26	0·158	2·53
71·6–81·5	20	77·8	1·29	34·6	27·4	64·0	3·55	1·15	0·147	2·55
81·6–84·6	20	82·8	1·32	36·7	30·2	63·5	2·46	1·04	0·121	2·57
84·7–91·8	20	87·5	1·40	40·8	33·6	62·5	2·40	0·58	0·064	2·61
22·3–91·8	140	65·2	1·30	25·4	23·1	60·9	6·07	1·14	0·141	2·54
Soils with > 2·00% organic carbon										
11·9–39·7	16	27·1	1·14	1·1	12·0	48·3	8·82	3·26	0·369	2·37
40·3–51·0	16	46·1	1·12	2·2	17·9	53·1	5·17	2·83	0·310	2·43
51·2–81·9	17	59·3	1·17	10·1	22·2	56·0	3·45	2·64	0·267	2·45
11·9–81·9	49	44·5	1·14	4·6	17·5	52·5	5·76	2·90	0·314	2·42

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TABLE 7

Effects of percentage of organic matter on soil properties

Range organic carbon %	Number of soils	Organic carbon Mean %	Bulk density g/ml (< 2 mm soil)	Instability I/WS %	Instability I/DS %	Instability I/MS %	Breaking strength kg	Particles 6–0·02 mm %	Total nitrogen %	Absolute density g/ml
All soils										
0·18–0·58	21	0·42	1·41	35·9	29·4	60·4	5·83	76·0	0·056	2·60
0·58–0·96	21	0·72	1·36	35·7	25·1	63·4	5·61	73·6	0·093	2·59
0·97–1·10	21	1·03	1·31	25·8	21·5	61·7	6·56	65·6	0·135	2·55
1·13–1·29	21	1·22	1·25	27·5	23·4	61·8	7·77	62·1	0·147	2·53
1·31–1·50	21	1·40	1·26	25·6	21·0	61·7	5·03	64·7	0·174	2·53
1·50–1·72	21	1·62	1·25	15·1	21·7	59·4	5·60	58·7	0·192	2·50
1·75–2·10	21	1·92	1·22	5·0	16·5	56·2	6·90	49·9	0·224	2·48
2·11–2·65	21	2·44	1·16	8·7	19·1	55·9	5·19	47·9	0·260	2·46
2·66–6·90	21	3·68	1·11	0·6	16·2	48·6	5·70	39·4	0·391	2·35
0·18–6·90	189	1·60	1·26	20·0	21·5	58·8	6·02	59·8	0·186	2·51
Arable soils including fallows and subsoils										
0·18–0·59	24	0·44	1·40	36·8	29·6	60·9	5·52	77·1	0·059	2·60
0·59–1·00	24	0·81	1·34	32·6	22·9	62·1	6·29	70·3	0·106	2·58
1·01–1·41	24	1·21	1·26	25·4	19·2	61·0	8·37	57·1	0·153	2·52
1·42–2·02	24	1·68	1·23	10·6	17·4	57·6	7·61	48·2	0·198	2·50
2·10–3·54	22	2·66	1·19	6·5	17·6	55·0	6·68	44·9	0·287	2·43
0·18–3·54	118	1·34	1·28	22·6	21·4	59·3	6·90	59·9	0·158	2·53
FYM, compost, and sewage sludge treated soils										
0·85–1·31	11	1·17	1·30	35·0	28·1	65·4	3·98	77·2	0·141	2·55
1·34–1·65	11	1·48	1·27	31·8	25·8	63·0	3·97	72·6	0·181	2·52
1·67–3·85	12	2·44	1·19	7·7	19·1	56·5	5·87	49·8	0·281	2·45
0·85–3·85	34	1·72	1·25	24·3	24·2	61·4	4·64	66·0	0·203	2·50
Grassland soils (permanent grass, leys, soils ploughed out of grass)										
1·02–1·50	12	1·20	1·29	19·7	23·8	61·1	4·83	65·4	0·148	2·56
1·68–2·25	12	1·91	1·20	2·7	17·9	56·1	5·11	55·8	0·221	2·49
2·30–6·90	13	3·82	1·04	1·2	17·9	46·0	4·12	41·9	0·391	2·35
1·02–6·90	37	2·35	1·17	7·7	19·8	54·2	4·67	54·0	0·257	2·46

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TABLE 8

Coefficients of correlations between physical tests on soils and their mechanical and chemical properties

	Coarse particles		Fine particles		Organic matter		
	6–0·02 mm %	6–0·2 mm %	silt %	clay %	C %	N %	coarse (2–6 mm) %
Bulk density (BD)							
Arable	0·42	0·41	−0·38	−0·17	−0·59	−0·62	−0·34
Grass	0·42	0·35	−0·27	0·04	−0·84	−0·76	−0·61
All	0·44	0·40	−0·36	−0·16	−0·70	−0·70	−0·49
Water holding capacity (WHC)							
Arable	−0·63	−0·53	0·36	0·52	0·65	0·66	0·37
Grass	−0·57	−0·39	0·34	0·17	0·86	0·90	0·40
All	−0·61	−0·48	0·33	0·46	0·74	0·76	0·44
Water slaking instability (I/WS)							
Arable	0·80	0·73	−0·56	−0·62	−0·64	−0·68	−0·28
Grass	0·50	0·54	−0·35	−0·31	−0·50	−0·55	−0·43
All	0·72	0·63	−0·48	−0·55	−0·63	−0·68	−0·37
Dry slaking instability (I/DS)							
Arable	0·83	0·79	−0·64	−0·63	−0·35	−0·46	−0·16
Grass	0·81	0·69	−0·68	−0·74	−0·30	−0·47	0·03
All	0·78	0·69	−0·59	−0·61	−0·36	−0·48	−0·13
Total mechanical slaking (I/MS)							
Arable	0·57	0·52	−0·35	−0·48	−0·44	−0·44	−0·11
Grass	0·61	0·39	−0·49	−0·14	−0·80	−0·86	−0·29
All	0·58	0·49	−0·38	−0·40	−0·62	−0·63	−0·26
Breaking strength (BS)							
Arable	−0·73	−0·63	0·47	0·69	0·05	0·15	−0·01
Grass	−0·36	−0·42	−0·35	0·61	−0·34	−0·27	−0·23
All	−0·61	−0·57	0·40	0·62	−0·12	−0·03	−0·11

density decreasing as carbon increased. By contrast, clay and silt contents had little effect on bulk density (Table 8). Silt usually behaved in much the same way as clay, though most relationships were less closely correlated than for clay. (The silt content rarely had independent effects on the results of the stability tests and it is not discussed in detail.) 'Coarse' organic matter (2–6 mm) rarely had large and significant effects on the properties measured and does not merit detailed discussion.

Water-holding capacity (WHC). The simple laboratory measurement of water-holding capacity at low tension was made on <2 mm soil; the values obtained always much exceed field capacity but they are quite reproducible. WHC diminished with increasing proportions of fine particles and increased linearly with increasing organic carbon contents—both for arable and grassland soils. The slaking in water of small aggregates affects the amount of water retained by the sample because it modifies interparticle voids and the tension between the soil particles. The soils were wetted long enough for the organic matter to become saturated.

The percentages of coarse particles (6–0·02 mm) were more closely correlated with WHC ($r = -0{\cdot}61$) than were the percentages CP (6 mm–0·2 mm) excluding fine sand ($r = -0{\cdot}48$). The negative correlation of coarse particles with WHC was much less

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TABLE 9

Coefficients of linear regression of physical and chemical properties on results of physical tests

	% Coarse particles (6–0·02 mm)				% Clay (< 0·002 mm)			
	b	SE	t	% Associated variance	b	SE	t	% Associated variance
Water slaking instability								
All	0·63	±0·045	14·04	51·1	−0·86	±0·096	8·98	29·8
Arable	0·65	±0·41	16·03	63·7	−0·88	±0·092	9·55	38·2
Grass	0·41	±0·119	3·43	23·0	−0·57	±0·293	1·93	7·1
Dry mechanical slaking								
All	0·34	±0·019	17·38	61·5	−0·47	±0·044	10·55	37·0
Arable	0·34	±0·019	18·22	69·4	−0·45	±0·045	9·86	39·7
Grass	0·37	±0·044	8·28	65·2	−0·75	±0·115	6·54	53·7
Total mechanical slaking								
All	0·22	±0·022	9·69	33·1	−0·27	±0·045	5·92	15·3
Arable	0·18	±0·021	8·40	32·3	−0·26	±0·039	6·66	22·9
Grass	0·35	±0·075	4·62	36·1	−0·18	±0·213	0·85	−0·8
Breaking strength								
All	−1·36	±0·128	10·67	37·5	2·47	±0·227	10·91	38·6
Arable	−1·57	±0·122	12·85	52·9	2·60	±0·224	11·63	47·9
Grass	−0·71	±0·305	2·31	10·8	2·65	±0·583	4·55	35·4
Bulk density								
All	0·28	±0·042	6·73	19·0	−0·19	±0·083	2·28	2·2
Arable	0·24	±0·043	5·54	16·9	−0·17	±0·082	2·07	2·2
Grass	0·35	±0·128	2·75	15·4	0·08	±0·317	0·24	−2·7
Water holding capacity								
All	−0·52	±0·049	10·48	36·6	0·71	±0·099	7·17	21·1
Arable	−0·46	±0·048	9·75	39·2	0·67	±0·091	7·39	26·9
Grass	−0·67	±0·165	4·09	30·4	0·45	±0·440	1·02	0·1
	% Organic carbon				% Total nitrogen			
Water slaking instability								
All	−10·35	±0·923	11·21	39·9	−110·10	±8·63	12·75	46·2
Arable	−12·77	±1·25	10·19	41·3	−121·79	±11·01	11·06	45·4
Grass	−4·55	±1·30	3·41	22·9	−54·95	±14·03	3·92	28·5
Dry mechanical slaking								
All	−2·85	±0·545	5·22	12·3	−37·91	±5·06	7·49	22·7
Arable	−3·50	±0·769	4·55	11·9	−42·01	±6·63	6·34	21·1
Grass	−1·50	±0·80	1·80	6·6	−26·11	±8·26	3·16	20·0
Total mechanical slaking								
All	−4·35	±0·397	10·96	38·8	−43·29	±3·91	11·06	39·2
Arable	−3·36	±0·565	5·94	19·0	−30·45	±5·16	5·90	18·8
Grass	−5·01	±0·623	8·03	63·8	−59·80	±6·00	9·96	73·2
Breaking strength								
All	−5·18	±2·98	1·74	1·1	−12·15	±29·73	0·41	−0·4
Arable	2·52	±4·32	0·58	−0·4	73·70	±38·94	1·89	1·7
Grass	−7·24	±3·37	2·15	9·1	−64·07	±38·60	1·66	4·6
Bulk density								
All	−8·46	±0·621	13·53	49·2	−82·40	±6·19	13·31	48·4
Arable	−8·25	±0·934	8·83	34·5	−78·40	±8·30	9·44	37·6
Grass	−7·66	±0·849	9·02	69·1	−77·70	±11·27	6·89	56·4
Water holding capacity								
All	11·76	±0·770	15·27	55·2	119·42	±7·34	16·27	58·4
Arable	11·65	±1·14	10·24	41·6	108·84	±10·16	10·71	43·8
Grass	11·19	±1·10	10·16	73·9	129·78	±10·87	11·93	79·7

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TABLE 10

Correlation coefficients between results of physical tests on arable and grassland soils

	Slaking tests			Breaking strength of soil cylinders (BS)	Bulk density (BD)	Water-holding capacity (WHC)
	Water (I/WS)	Dry (I/DS)	Total (wet + pressure) (I/MS)			
			Arable soils (145)			
I/WS	1·00	—	—	—	—	—
I/DS	0·71	1·00	—	—	—	—
I/MS	0·59	0·52	1·00	—	—	—
BS	−0·49	−0·67	−0·29	1·00	—	—
BD	0·53	0·30	0·28	−0·02	1·00	—
WHC	−0·71	−0·56	−0·46	0·34	−0·55	1·00
			Grassland soils (45)			
I/WS	1·00	—	—	—	—	—
I/DS	0·38	1·00	—	—	—	—
I/MS	0·51	0·44	1·00	—	—	—
BS	0·10	−0·54	0·28	1·00	—	—
BD	0·59	0·14	0·69	0·42	1·00	—
WHC	−0·63	−0·28	−0·79	−0·42	−0·81	1·00

than the positive correlations with % organic carbon ($r = 0{\cdot}74$) or with % total nitrogen ($r = 0{\cdot}76$). As with bulk density, water-holding capacity was little influenced by differences in the form of organic matter caused by manuring or by a history including grassland.

Slaking by water (I/WS). This, the most important of the measurements made, shows whether soil aggregates are stable when wetted, and lose only trivial amounts of pore space, or whether they slake to release individual particles, become compact and lose much pore space. Most soils with much coarse material (>0·02 mm) slake nearly completely; residual pore space, on which aeration and drainage depend, is then determined by relative proportions of coarse and fine materials and by the irregularities in packing. When the fine particles are completely released and are enough to fill the pores between gravel, coarse and fine sand, slaking can be disastrous because, with pores completely occupied by solids, no space is left for air and water. This can happen with sandy clay soils, in which sand is enough to separate the clay and prevent it acting as a cement to give stable aggregates, and clay and silt are enough to fill the spaces between the sand particles. The upper limit of loss in pore space in the water slaking test is about 70%. This was empirically measured on ranges of sand particles artificially aggregated by a strong sucrose solution and then tested in the water instability apparatus of Williams and Cooke (1961); the aggregates were, of course, completely unstable when wetted. The one-third of pore space remaining varies slightly with shape of particles and their packing characteristics, and whether they can move and resort. Particles helped to move by mechanical agitation, or by moving water, can pack more closely.

In Table 11 the soils are grouped by the loss in pore space on water slaking. The soils become more unstable as percentages of gravel + coarse sand + fine sand (6–0·02 mm) increase and as silt + clay diminishes. The most stable soils tend to contain most organic carbon (nearly three times as much as the very unstable soils). Soils that lost no more than one-tenth of their pore space when wetted contained, on average, 1·5% organic carbon.

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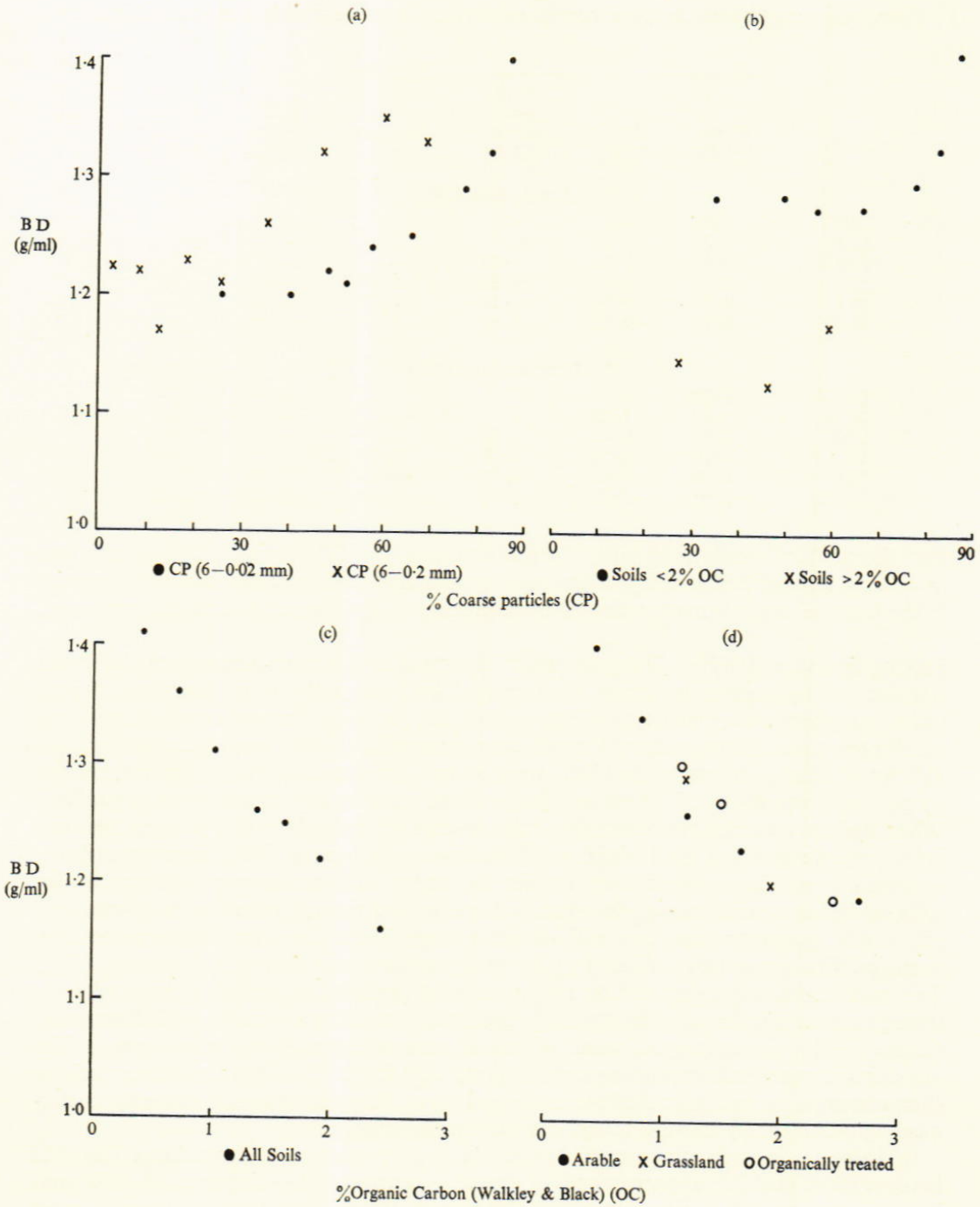

Fig. 1. The effect of soil composition upon the bulk density of <2 mm soil.

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TABLE 11

Groups of soils arranged by their instability in water, and average mechanical compositions of the groups

Number of soils	Water slaking instability % loss in pore space	Mechanical composition: Coarse particles (6–0·02 mm)	Silt (0·02–0·002 mm)	Clay (< 0·002 mm)	Organic carbon %
55	(−2 to +5)	44·0	21·7	21·2	2·57
26	(+5 to +15)	51·6	20·3	18·2	1·55
33	(+15 to +25)	51·9	21·6	17·9	1·44
44	(+25 to +40)	75·6	9·9	9·2	1·02
30	(+40 to +70)	77·7	8·5	8·4	0·93

The two constituents that had most effect on slaking are easily determined. Gravel and sand fractions (6–0·02 mm), when large, dominate physical properties and their amounts should always be measured in work on physical properties. The simple 'Walkley and Black' method for organic carbon measures the readily oxidisable organic matter in soils (Bremner & Jenkinson, 1960) which is most likely to stabilise aggregates. An example of the greater value of this measure than of total carbon was shown by one soil in this series that contained 0·5% C by the Walkley and Black method, the water slaking instability was 15% (which is large for a clay loam). Combustion analysis showed that it contained 3% total carbon; clearly most was in very resistant forms having little influence on soil stability.

As was expected, grassland soils were, on average, much more stable than arable soils and the range of instabilities measured was smaller (Table 3). Grassland soils with more than 1·5% C were almost completely stable; groups of arable soils with as much organic carbon were unstable and there was little differences between the arable soils whether or not they had received organic manures (Fig. 2c).

Tables 5 and 6 and Fig. 2 examine the effects of increasing amounts of sand and gravel on water stability. Soils nearly devoid of gravel and coarse sand were unstable; the most stable group had 10–15% of particles in the 6–0·2 mm range, and the least stable had half or more in this fraction. A quarter of the soils had more than 2% carbon; as a group, these were very stable, and the mechanical composition had little effect (Fig. 2b). Table 6 includes fine sand (0·2–0·02 mm) in the 'coarse' fraction. The general increase in stability with diminishing proportions of coarse particles (6–0·02 mm) is still clear, but including fine sand diminishes contrasts between groups of soils (Fig. 2a). This suggests that the division between coarse and fine sand has important effects on stability; small proportions of fine sand tend to behave as silt and clay but when fine sand is a major fraction, soils are less stable. However, the correlation coefficients in Table 8 suggest that instability of arable soils is better related to amount of coarse particles, including fine sand, than to the 6–0·2 mm fraction alone. In the 'grassland' soil group, including fine sand had little effect. Organic carbon (and total N) and clay content were also well related to stability of the arable soils to water, but relationships were less in grassland soils (Tables 8 and 9). Per cent silt was nearly as important as % clay in making aggregates more stable (Table 8). Amount of coarse organic matter (i.e. recent remains of plants or organic manures) was related to stability, especially of grassland soils.

Linear regression coefficients (Table 9) show that about a third of the total variance in water instability of arable soils was associated with clay contents, but much less for the grassland soils. More than 40% of variance in the instability of arable soils was associated

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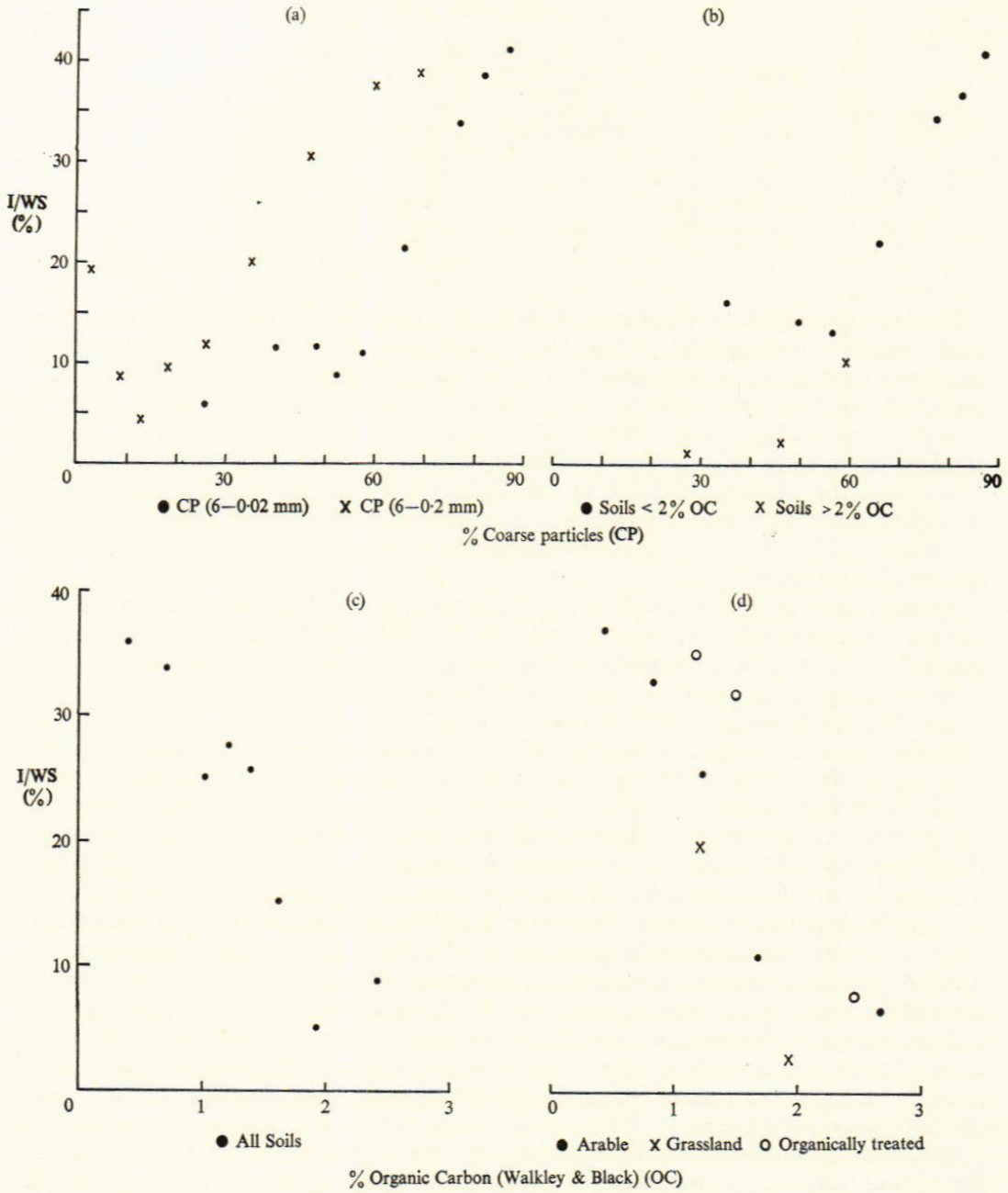

Fig. 2. The effect of soil composition upon the water slaking instability of 4–6 mm aggregates.

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with organic carbon, the proportion was less for grassland soils; %N was better related to instability than %C by the Walkley-Black method. Although the percentage of 'coarse' (2–6 mm) organic matter was significantly related to stability, the general relationship was poor.

The damage that wetting does to soil structure is related to the blocking of remaining pores by fine particles released by initial slaking. The movement of sand released in the instability test was observed through a hand lens while the aggregates in the glass tubes were being immersed; Table 12 summarises the information gathered. Ten categories of instability were gauged by the intensity of the slaking and the extent to which slaked particles became detached from the aggregates and were resorted; resorting did not occur until 16–21 % of pore space was lost on water slaking. Field soils are also exposed to the kinetic energy of falling raindrops. Soils in which particles move and with instabilities exceeding 15%, are likely to 'cap' in rain by surface pores becoming blocked by mobile particles. It is difficult to gauge instability visually, because some soils swell rapidly on wetting but the partially-slaked fragments cohere. However, observing slaking of aggregates under a low power microscope was useful for grading the instability of very small samples or individual aggregates.

TABLE 12

Per cent water slaking instability and associated visual slaking appearance

Observed		Associated mean I/WS	Associated % coarse particles (6–0·02 mm)	Associated % organic carbon (W & B)	Empirical stability scale
Slaking	Resorting				
None	None	0·2	54·5	3·23	Very stable
Slight	None	1·4	48·8	2·32	Stable
Moderate	None	8·3	52·1	1·91	Slightly unstable
	Very small	16·0	55·2	1·73	
	Small	21·9	63·3	1·41	
Much	None	24·9	61·5	1·26	Moderately unstable to unstable
	Very small	26·6	65·0	1·39	
	Small	31·7	65·4	1·06	
	Much	41·7	66·7	1·02	
Complete	Complete	46·9	76·5	0·70	Very unstable

Dry slaking by mechanical pressure (I/DS). The dry slaking test, in which dry aggregated soil is compressed in a tube (with a pressure of 7 kg/cm^2), simulates the damage caused by pressure from tractor and other wheels, or soil-working tools (which also smear the soil). The values reported are the percentage diminutions in total pore space. Water slaking and dry mechanical slaking were related, though not very closely ($r = 0{\cdot}70$ for arable soils, 0·38 for grassland soils). Instability diminished with increasing organic matter content (Table 7 and Fig. 3) though organic matter had much less effect on stability than on water slaking. Arable soils in the group richest in organic matter were nearly twice as stable as those with least (Table 7). Loss of pore space in the test increased with increasing percentages of coarse material in the soils; losses were more than twice as great in the group of soils with most coarse particles as in the group with least (Table 6). These relationships were more evident when fine sand was included in the coarse fraction of soil (Tables 5 and 6 and Fig. 3a).

Soils rich in organic matter were nearly as much affected by compression as were those with little organic matter (Fig. 3d). The close relationship between diminishing resistance

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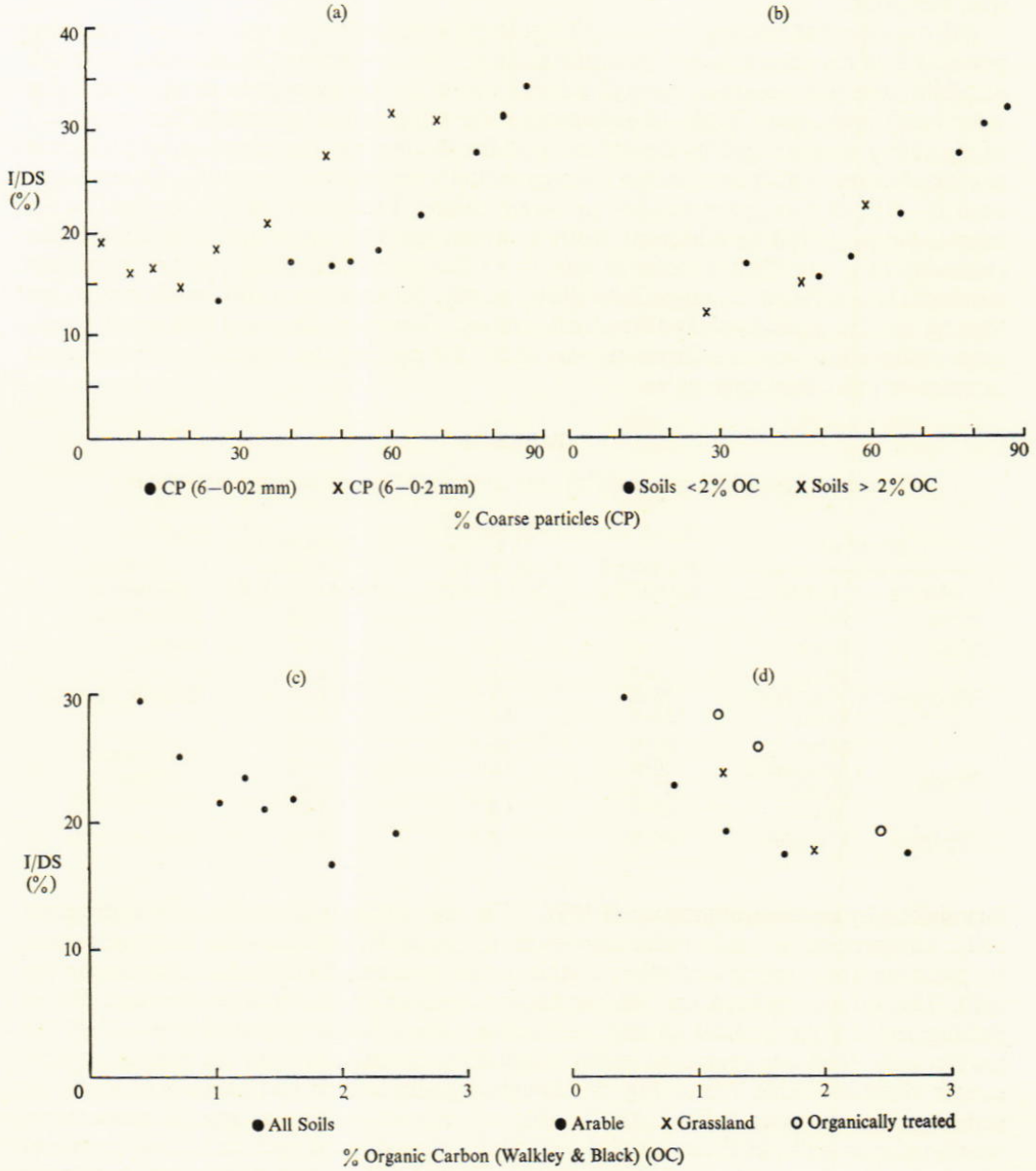

Fig. 3. The effect of soil composition upon the dry mechanical slaking of 4–6 mm aggregates.

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of air-dried aggregates to mechanical force and increasing amounts of coarse mineral fractions is illustrated well in Table 8, which shows little difference between groups of arable and grassland soils. The form or amount of organic matter had much less effect on mechanical resistance than on water slaking. Clay and silt had larger effects than organic matter in making aggregates stronger in the arable soils, and were even more effective in the grassland soils; both fractions had much less effect than coarse particles. Linear regression coefficients in Table 9 summarise these effects numerically. Tables 8 and 9 both show that the percentage of nitrogen was better related to the effects of dry mechanical slaking than % organic carbon, although %N only accounted for 20% of the variance.

Total mechanical slaking (I/MS). Results of this test, which measured the combined effects of water and mechanical slaking, indicate how damaging traffic over, or cultivation of, wet soils can be. Losses in pore space always exceeded those by water or dry mechanical slaking alone (Table 3). Even large increases in organic matter had only small effects on the stability of aggregates of arable soils; the organic matter in grassland soils had larger effects (Table 7). All the groups of soils resisted compression less as the proportions of coarse mineral particles increased (Tables 5 and 6 and Fig. 4). The relationship of proportion of coarse particles with total instability was altered little by including or omitting fine sand from the fraction (Fig. 4a and Tables 8 and 9). Organic matter (and % total N) had much larger effects on strength of aggregates from grassland than on those from arable soils (Tables 8 and 9 and Fig. 4d). Increasing organic matter (and total N) were associated with stronger aggregates from grassland soils, but less closely for aggregates from arable soils (Table 8). Indeed, Fig. 4d shows that the arable soils given organic manures were compressed much more easily than those not so manured.

Measurements on the cylinders of soil remaining after mechanical compaction showed that 95% of the arable soils had been compressed to at least 90% of the maximum depth possible; only a fifth of the grassland soils were compressed as much, as the lower ends of the cylinders were only slightly compacted. In two-thirds of the grassland soils the cylinders formed retained at least 30% of their volume in an uncompacted state. The roots left by grassland have a specific effect in helping soils resist damage by water and pressure; this effect was not achieved in the arable soils by organic manuring that had increased % organic carbon but not the coarse organic matter.

Breaking strength (BS). Clods are formed by cultivating heavy soil when it is so wet that the soil mass is compressed and smeared instead of being broken. It is important that any clods formed should be broken easily and the breaking strength test was developed to see how easily damage to structure caused by compressing wet soil could be repaired. The soil cylinders from the combined slaking and compression test were air-dried, a 25 mm section taken, and the force needed to split it under standard conditions measured.

Cylinders formed from the arable soils were mostly stronger than those from grassland; strength diminished rapidly as the proportions of coarse material in the soils increased (Tables 5 and 6 and Figs. 5a and 5b). There was no clear relationship between organic carbon content and breaking strength of cylinders for the whole group of soils (Table 7 and Fig. 5c). Dividing the soils into groups with more or less than 2% organic carbon, showed how the factors interacted. For any mechanical composition of soil, decreasing organic matter was associated with stronger cylinders (Fig. 5b). (In addition % clay and % organic carbon tended to increase together.) Fig. 5d divides the soils into groups with

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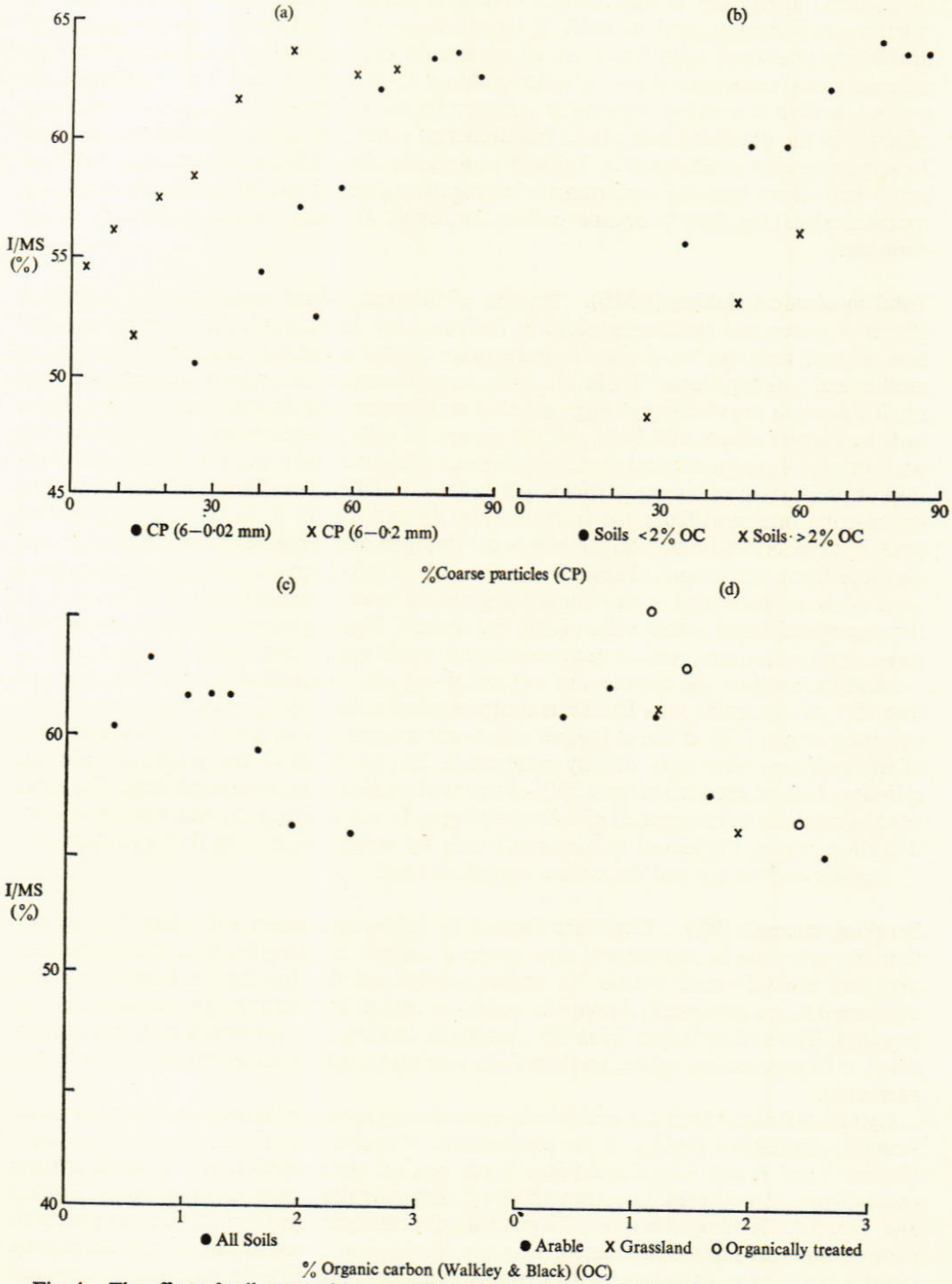

Fig. 4. The effect of soil composition upon the total mechanical slaking of 4–6 mm aggregates.

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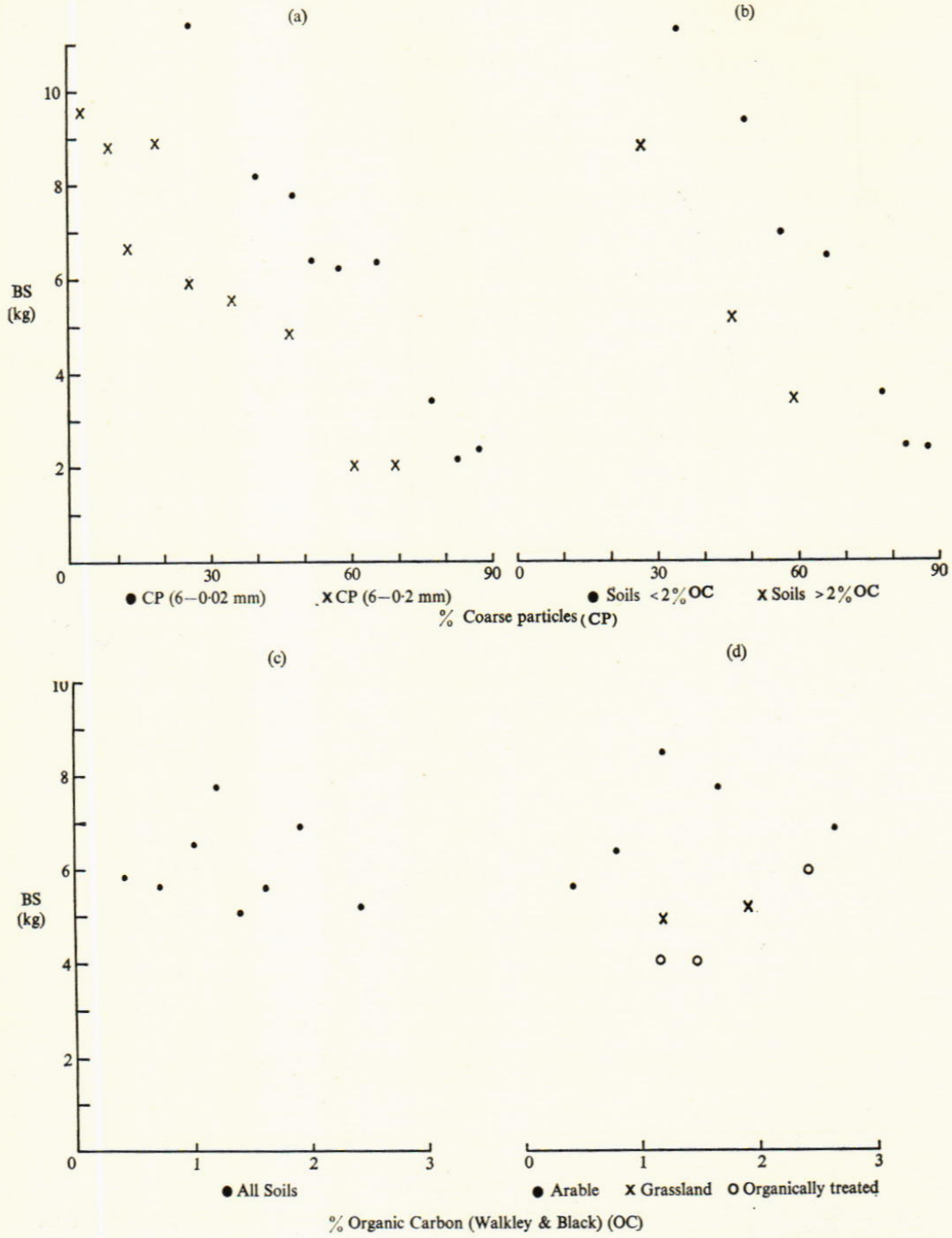

Fig. 5. The effect of soil composition upon the breaking strength of soil cylinders.

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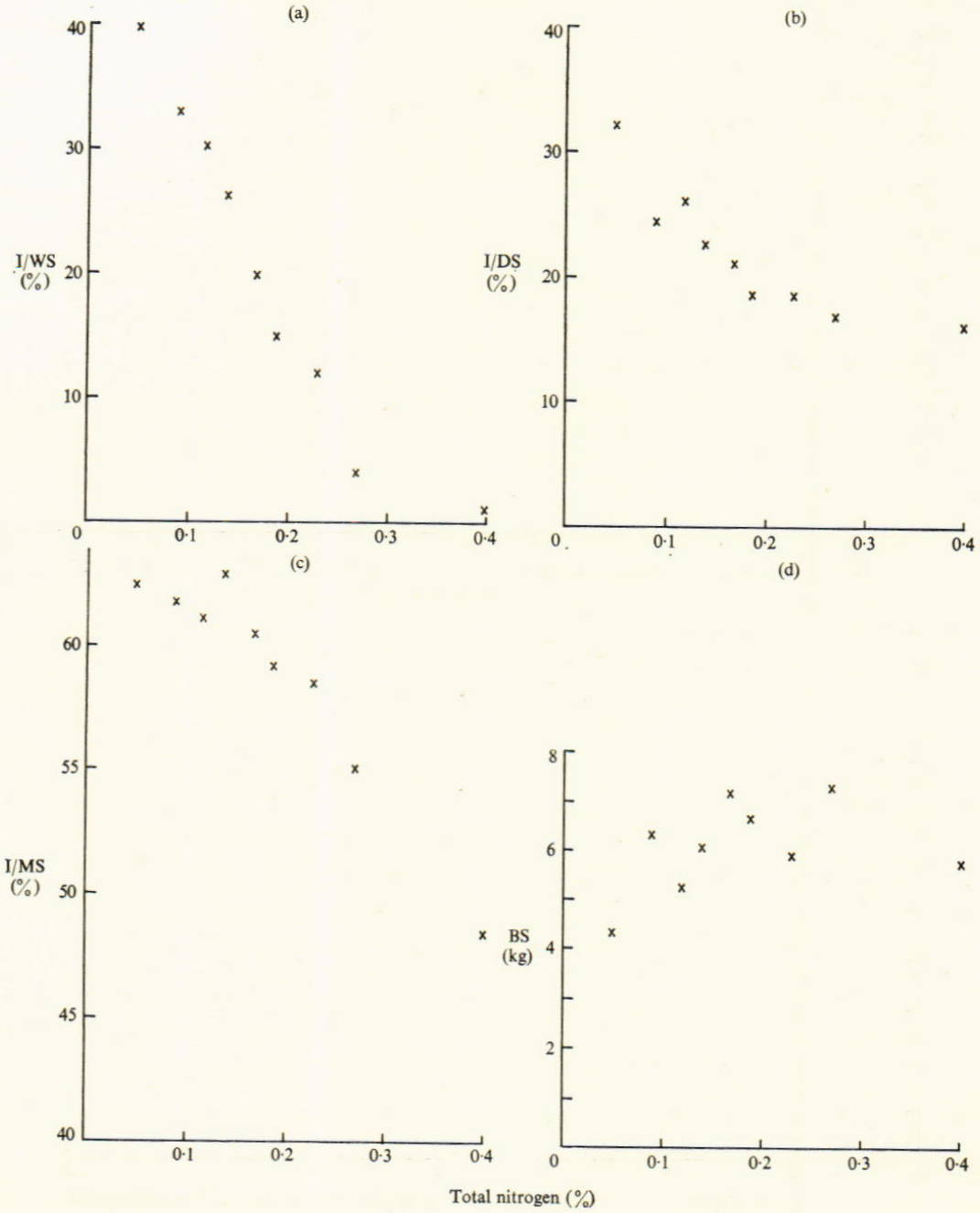

Fig. 6. The effect of percentage of total nitrogen upon water slaking instability, dry and total mechanical slaking, and breaking strength of soil cylinders.

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contrasted histories. Arable soils were strongest with about 1·2% carbon; grassland soils were usually less strong, and their strength diminished slightly with increasing carbon content. Increases in clay content made both arable and grassland soils much stronger (Table 8).

Relationships of soil nitrogen with results of physical tests. Unexpectedly, %N in soil was better correlated with results of many of the physical tests than was % organic carbon measured by the Walkley-Black method. Figure 6 shows relationships between % total N in the soils and the three measurements of instability and the one of strength of soils.

Instability in water was roughly linearly related to nitrogen content in the range 0·28–0·05% N (Fig. 6a); the relationship with % organic carbon (Fig. 2c) was of the same form, but less precise than with %N. The loss in pore space on dry mechanical slaking was also better related to %N than to % carbon, as also was total mechanical slaking (compare Figs. 4c and 6c). Neither carbon nor nitrogen contents were significantly related to the breaking strengths of soil cylinders. The scatter of points in the plot with organic carbon (Fig. 5c) indicates no relationship at all with breaking strength; Fig. 6d suggests, that, as %N increases, so does soil strength.

Per cent N seems to be better related than contents of organic carbon to the organic matter fraction that is active in stabilising soil structure: %N is easily determined and should be used in work that relates soil physical properties to organic matter contents.

Effects of interactions of soil properties on results of the physical tests

The results of the physical tests were rarely influenced by one factor alone. The commonest combination of properties acting together was percentage of coarse particles and percentage of organic matter, but clay content also interacted with other properties. The interactions of mechanical composition and organic matter content are complex and differ greatly from soil to soil. Correlation and regression analyses summarised in Tables 8 and 9 were used to select soil composition variates for partial regression analyses. Very many analyses were made, and those that removed the most variance are summarised here.

For the soils as a whole the partial regressions calculated removed half to two-thirds of the variance. Combinations of % coarse particles (6–0·02 mm) with % organic carbon removed about three-quarters of the variance in the water slaking and dry slaking tests on arable soils but were less successful on grassland soils. None of the variates examined explained total instability (mechanical + water slaking) of arable soils, but %N alone accounted for three-quarters of the variance in grassland soils. Combinations of % coarse particles plus a measure of the organic matter accounted for about two-thirds of the variance in breaking strength of soil cylinders and were roughly equally successful with arable and grassland; 'organic matter' was best measured by % total N.

Variations in bulk densities of the arable soils were not easily accounted for by regressions involving mechanical composition and organic matter, but %N and %C accounted for two-thirds of the variance in grassland soils. There were similar relationships in partial regression analyses involving water-holding capacity; mechanical composition and organic matter could account for about half of the variance in arable soils but 80% of the variance in WHC of grassland soils was accounted for by changes in contents of total N.

The more basic physical properties measured on the <2 mm soil aggregates—bulk density and water-holding capacity—were best characterised by soil organic matter;

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the coarse mineral fractions were less important. All the other measurements on arable soils involved tests on 4–6 mm aggregates that deformed the soil; successful partial regressions involved both coarse particles (6–0·02 mm) and organic matter; clay and silt were usually unimportant.

Partial regression analyses on two soil properties

Partial regression analyses were made on the results of the physical tests and soil properties; equations accounting for the largest percentage of variance associated with each test were calculated in terms of the amounts of coarse and fine material in the mineral fraction and amounts of organic matter. Table 13 gives the percentages of total variance that were accounted for by each of the regressions.

TABLE 13

Partition of variance in physical measurements by partial regressions on soil composition

Variates	CP	Silt	Clay	OC	N	CP OC	CP N	Silt OC	Silt N	Clay OC	Clay N
						Water slaking instability (I/WS)					
Arable	64	30	38	41	45	71	70	56	57	59	59
Grass	23	10	(7)	23	28	(28)	(29)	(24)	(27)	29	(30)
All	51	23	30	40	46	61	61	49	52	55	56
						Dry slaking instability (I/DS)					
Arable	69	41	40	12	21	(70)	(69)	44	47	41	44
Grass	65	45	54	(7)	20	69	(66)	(43)	(45)	60	62
All	61	35	37	12	23	(62)	(61)	38	42	41	44
						Total mechanical slaking (I/MS)					
Arable	32	12	23	19	19	35	(33)	24	23	31	29
Grass	36	22	(0)	64	73	(66)	(72)	(67)	(73)	(64)	(73)
All	33	14	15	39	39	48	45	42	42	44	42
						Breaking strength (BS)					
Arable	53	21	48	(0)	(2)	67	65	(22)	(21)	52	50
Grass	11	10	35	9	(5)	57	67	36	36	48	53
All	37	16	39	(1)	(0)	63	62	22	19	47	46
						Bulk density (< 2 mm soil) (BD)					
Arable	17	14	2	34	38	36	(38)	39	40	(34)	38
Grass	15	(5)	(0)	69	56	(69)	(58)	(68)	(57)	(69)	61
All	19	13	2	49	48	(50)	(48)	51	49	(49)	49
						Water holding capacity (< 2 mm soil) (WHC)					
Arable	39	13	27	42	44	53	52	44	45	51	51
Grass	30	9	(0)	74	80	(74)	(80)	(73)	(81)	(75)	(79)
All	37	11	21	55	58	62	62	56	(58)	63	62

CP = % Coarse particles (6–0·02 mm)
OC = % Organic carbon (Walkley & Black)
N = % Total nitrogen
Silt = % Silt (0·02–0·002 mm)
Clay = % Clay (< 0·002 mm)
( ) = Regression not significant

The analyses included comparisons of the coarse soil fraction expressed as gravel + coarse + fine sand (6–0·02 mm) and with the coarse fraction omitting fine sand. The wider range (6–0·02 mm) was always more closely related for arable soils and results for gravel + coarse sand (i.e. 6–0·2 mm) are not given in Table 13 or discussed further except in connection with equations for bulk density and water slaking. Per cent organic carbon and %N were roughly interchangeable as measures of active organic matter in the soils.

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Of all the factors examined 'coarse organic matter' (separated mechanically from the soils) in the range 2–6 mm, was least associated with the results of the tests on the soils. It had little or no relationship to results of the tests on dry slaking and total slaking, or on breaking strength of soil cylinders. Measurements of coarse organic matter were associated with 7% of variance in water-slaking tests on arable soil and with 16% for the grassland soils, much less than for other properties measured. The results of regression analyses involving coarse organic matter are therefore not included in Table 13. The contents of both silt and clay were included in the regressions. Per cent clay had important effects in many of the equations. Results with % silt were much less useful; the fraction rarely had an independent part, often it behaved as clay but was less well correlated with the results of physical tests, and sometimes it seemed nearly inert. Some results of equations including silt are in Table 13, but they are not discussed in detail. Effects of single soil properties and combinations of two properties are discussed below for each of the measurements. Regression equations are stated, together with the standard errors of their components, the residual mean squares, and the percentage of variance accounted for by regression. Three groups of 13 arable, grassland and 'mixed' soils, selected to give the widest range of coarse particles (6–0·02 mm), were used to test by substitution in the equations in the following sections:

Bulk density (BD)

Arable soils. Organic matter content (%C or %N) accounted for a third of the variance and there was only little improvement by taking account of the coarse or fine mineral fraction. The linear regression accounting for 38% of the variance was:

$$\text{BD (g/ml)} = 1{\cdot}42\ (\pm 0{\cdot}017) - 0{\cdot}78\ (\pm 0{\cdot}083)\ (\%\ \text{Total N})$$

Residual mean square 0·008 (145 d.f.).
For arable soils the mean bulk density calculated was 1·25 and 1·26 found. (Coarse organic matter accounted for 11% of variance.)

Grassland soils. Organic carbon accounted for 69% of variance; the best equation was:

$$\text{BD (g/ml)} = 1{\cdot}37\ (\pm 0{\cdot}025) - 0{\cdot}076\ (\pm 0{\cdot}008)\ \%\text{OC}$$

Residual mean square 0·005 (35 d.f.).
The mean bulk density for grassland soils was calculated as 1·16 against a mean of 1·14 found. There was no improvement for grassland soils from regression analyses incorporating the mineral fractions, but coarse matter alone was associated with 36% of the variance.

All soils. The proportions of coarse particles were associated with a fifth of the variance and organic matter with half; clay was not related (there was some relationship with % silt). Constants in the regression equations with organic matter and coarse particles as single factors are in Table 9; the best equation for the whole group of soils involved coarse particles (CP) gravel + coarse sand (6–0·2) mm, and organic carbon and associated with 52% of the variance, was:

$$\text{BD (g/ml)} = 1{\cdot}360\ (\pm 0{\cdot}18) + 0{\cdot}001\ (\pm 0{\cdot}0003)\ \%\text{CP (6–0·2 mm)} - 0{\cdot}076\ (\pm 0{\cdot}0065)\ \%\text{OC}$$

Residual mean square 0·008 (186 d.f.).

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Average calculated and measured bulk densities for all soils examined were the same, 1·28.

Water holding capacity (WHC)

Arable soils. About 40% of the variance in water holding capacities of the arable soils was associated with the coarse fraction of the soils and 40–50% with the organic matter content. Per cent OC and %N were associated with about three-quarters of the variance for grassland soils. Clay accounted for a quarter of the variance for arable soils and was not associated with variance in the grassland soils. Silt accounted for an eighth or less of the variance in the whole group of soils. Combinations of organic carbon and either coarse particles or clay accounted for about half of the total variance.

The best equation (associated with 53% of the variance) was:

$$\%\text{WHC} = 53{\cdot}2\ (\pm 4{\cdot}31) - 0{\cdot}30\ (\pm 0{\cdot}049)\ \%\text{CP (6–0·02 mm)} + 7{\cdot}93\ (\pm 1{\cdot}18)\ \%\text{OC}$$

Residual mean square 103·8 (144 d.f.).

Average WHC calculated from the equation was 51·0% (against 46·1% measured).

Grassland soils. Organic matter (expressed as %N) accounted for the 80% of the variance; the equation was:

$$\%\text{WHC} = 24{\cdot}2\ (\pm 3{\cdot}31) + 129{\cdot}8\ (\pm 10{\cdot}87)\%\ \text{Total N}$$

Residual mean square 72·3 (35 d.f.).

The mean calculated value of WHC for the selected soils was 64·6% (against 67·6% measured). There was no improvement from taking account of the mineral fractions. Coarse particles accounted for a third of the variance, but clay for none.

All soils. Organic matter accounted for over half of the variance, smaller proportions being associated with % coarse particles or with % clay. The equation accounting for most (62%) variance was:

$$\%\text{WHC} = 49{\cdot}2\ (\pm 3{\cdot}65) - 0{\cdot}26\ (\pm 0{\cdot}044)\%\ \text{CP (6–0·02 mm)} + 9{\cdot}27\ (\pm 0{\cdot}82)\%\ \text{OC}$$

Residual mean square 104·6 (186 d.f.).

Using this equation to calculate WHC gave an average of 48·1% WHC, compared with the average of measured values 49·7% WHC.

An alternative, equally successful equation accounting for 63% variance, included the clay fraction (which, of course, increases as coarse particles diminish):

$$\%\text{WHC} = 24{\cdot}2\ (\pm 1{\cdot}63) + 10{\cdot}55\ (\pm 0{\cdot}73)\%\ \text{OC} + 0{\cdot}43\ (\pm 0{\cdot}07)\%\ \text{Clay}$$

Residual mean square 103·4 (186 d.f.).

Calculated average WHC was 48·5% (the average of measured values was 49·7%).

Water slaking (I/WS)

Arable soils. Two-thirds of the total variance in % loss in pore space on water slaking was associated with percentage of coarse particles. Clay was also associated with a third of the variance and organic matter with rather more. Regressions involving both coarse particles and organic matter accounted for 70% of the variance for arable soils.

Most variance (71%) for arable soils was removed by this equation:

$$\%\text{I/WS} = 0{\cdot}49\ (\pm 3{\cdot}73) + 0{\cdot}52\ (\pm 0{\cdot}042)\%\ \text{CP (6–0·02 mm)} - 6{\cdot}34\ (\pm 1{\cdot}02)\%\ \text{OC}$$

Residual mean square 77·6 (144 d.f.).

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Grassland soils. Only a quarter of the variance was accounted for by the coarse fraction (6–0·02 mm). Slightly more variance (38%) was removed by including % coarse particles (6–0·2 mm) with % total nitrogen. The best equation for grassland soils was:

$$\%I/WS = 12{\cdot}9\ (\pm 5{\cdot}53) + 0{\cdot}22\ (\pm 0{\cdot}086)\%\ CP\ (6\text{–}0{\cdot}2\ mm) - 39{\cdot}4\ (\pm 14{\cdot}33)\%\ Total\ N$$

Residual mean square 103·5 (34 d.f.).
The average calculated value of I/WS using the equation was 4·7% against 0·4% measured. This poor agreement, and the failure to remove more variance in water instability tests on grassland soils, are both explained by the difficulty with this slaking test of assessing very small losses in pore space in groups of soils that are very stable to water (but the alternative method of Williams (1963) does differentiate well between small instabilities).

All soils. Percentage of coarse particles and % organic carbon were both important; the best equation, accounting for over 60% of total variance, was:

$$\%I/WS = 2{\cdot}47\ (\pm 3{\cdot}85) + 0{\cdot}47\ (\pm 0{\cdot}047)\%\ CP\ (6\text{–}0{\cdot}02\ mm) - 5{\cdot}95\ (\pm 0{\cdot}87)\%\ OC$$

Residual mean square 116·4 (186 d.f.).
Using this equation gave an average of 19·5% I/WS (average of measured values was 19·0%).

Dry slaking (I/DS)

Arable soils. Variance in the pore loss on dry slaking was mostly accounted for by the proportions of coarse particles; the following equation accounted for 69% of the variance:

$$\%I/DS = 0{\cdot}71\ (\pm 1{\cdot}21) + 0{\cdot}34\ (\pm 0{\cdot}019)\%\ CP\ (6\text{–}0{\cdot}02\ mm)$$

Residual mean square 20·7 (145 d.f.).
(The average calculated value of I/DS was 19·3% compared with 20·9% measured.) Relationships with % clay (and with % silt) were less close, also with organic matter.

Grassland soils. These soils behaved similarly. The following equation accounted for 69% of the variance:

$$\%I/DS = -\ 6{\cdot}79\ (\pm 3{\cdot}87) + 0{\cdot}43\ (\pm 0{\cdot}051)\%\ CP\ (6\text{–}0{\cdot}02\ mm) + 1{\cdot}25\ (\pm 0{\cdot}57)\%\ OC$$

Residual mean square 16·3 (34 d.f.).
The average calculated values of I/DS for grassland soils was 18·9% and the average measured was 19·9. Percentage of clay was associated with 54% of the variance, and % coarse particles with 65%; silt was less important.

All soils. Equations combining mineral composition with other factors in partial regressions analyses removed no more variance than percentage of coarse particles alone. The best relationship associated with 61% variance was:

$$\%I/DS = 1{\cdot}41\ (\pm 1{\cdot}22) + 0{\cdot}34\ (\pm 0{\cdot}019)\%\ CP\ (6\text{–}0{\cdot}02\ mm)$$

Residual mean square 27·2 (187 d.f.).
Average I/DS calculated was 20·3%, average measured was 19·6%.

Total mechanical slaking (I/MS)

Arable soils. Coarse particles accounted for a third, clay for a quarter (silt was less important than clay) and organic matter for a fifth of the variance; there was little gain

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from regressions on more than one soil property. The most variance (35%) was accounted for by the equation:

$$\%I/MS = 53{\cdot}5\ (\pm 2{\cdot}15) + 0{\cdot}15\ (\pm 0{\cdot}024)\%\ CP - 1{\cdot}54\ (\pm 0{\cdot}59)\%\ OC$$

Residual mean square 25·9 (144 d.f.).
(The average I/MS calculated was 59% compared with 63% measured.)

Grassland soils. Percentage of coarse particles accounted for a third, but organic carbon for two-thirds and %N for three-quarters of the variance in I/MS; regressions on the two properties together removed no more variance than organic matter alone. The best equation associated with 73% variance for grassland soils was:

$$\%I/MS = 70{\cdot}7\ (\pm 1{\cdot}83) - 59{\cdot}8\ (\pm 6{\cdot}00)\%\ \text{Total N}$$

Residual mean square 22·0 (35 d.f.).
(The calculated average I/MS was 52%, compared with 53% measured.)

All soils. Coarse particles and organic carbon each accounted for about a third of the variance, and about 10% more was accounted for by a regression on the two properties. The best equation used, which did not involve quadratic or logarithmic functions, accounted for 48% of the variance and was:

$$\%I/MS = 56{\cdot}4\ (\pm 1{\cdot}90) + 0{\cdot}13\ (\pm 0{\cdot}023)\%\ CP\ (6\text{–}0{\cdot}02\ mm) - 3{\cdot}11\ (\pm 0{\cdot}43)\%\ OC$$

Residual mean square 28·2 (186 d.f.).
(Average I/MS for the whole *group of soils* calculated from this equation was 59%, the measured value was 62%.)

Breaking strength (BS)

Arable soils. Percentage of coarse particles or % clay each accounted for about half of the total variance in breaking strength of soil cylinders (silt was much less important); none was accounted for by the organic matter, measured as %OC or %N. Regressions of % coarse particles and % organic carbon *together* removed two-thirds of the variance. The most successful equation for arable soils was:

$$BS\ (kgm) = 22{\cdot}2\ (\pm 1{\cdot}05) - 0{\cdot}20\ (\pm 0{\cdot}012)\%\ CP\ (6\text{–}0{\cdot}02\ mm) - 2{\cdot}29\ (\pm 0{\cdot}29)\%\ OC$$

Residual mean square 6·15 (144 d.f.).

Grassland soils. The soils behaved differently: % coarse particles (and % silt) and % organic carbon each alone accounted for 10% or less of the variance; % clay was associated with about a third of the total variance. Interaction effects were clearly shown in regression equations combining coarse particles and organic matter, which accounted for two-thirds of the variance (using %N to measure organic matter). More variance was also removed in equations involving clay with organic matter, but these were less successful than those including coarse particles. The best equation for the grassland soils associated with 67% variance was:

$$BS\ (kg) = 22{\cdot}9\ (\pm 2{\cdot}16) - 0{\cdot}21\ (\pm 0{\cdot}026)\%\ CP\ (6\text{–}0{\cdot}02\ mm) - 24{\cdot}9\ (\pm 3{\cdot}22)\%\ \text{Total N}$$

Residual mean square 3·18 (34 d.f.).
(The calculated average value was 4·3 kg, against 4·1 kg measured.)

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All soils. Regression on % coarse particles and % organic matter removed most (over 60%) of the total variance. As with the separate groups, there were large interactions between these soil composition variates:

BS (kg) = 22·3 (±0·94) − 0·20 (±0·011) % CP (6–0·02 mm) − 2·43 (±0·21) % OC

Residual mean square 6·92 (186 d.f.).
The average calculated value was 7·6 kg compared with 8·0 kg measured.

Regressions on more than two soil properties

Further regression analyses were made involving more than two soil properties and their logarithms and squares. Some of these equations accounted for more variance than partial regressions involving two properties, but most of the regressions were not significant ($P = 0{\cdot}05$) and are not discussed here. Table 14 lists results from some of the equations involving three variates and compares the variance removed with that accounted for in the simpler regressions. Although some of the more complicated regressions removed a little more variance than those with only one or two variates, the gain was not commensurate with the extra work. It seems possible to account for most of the variance in these physical tests on soil only where one soil property dominates the results, as where % coarse particles determines amounts of wet or dry slaking of arable soils, or where % organic matter determines water-holding capacity of grassland soils. It was rare for two contrasted properties considered together to account for *much* more variance in the physical measurements discussed here than each property considered separately; it was very rare to account for much more than three-quarters of the total variance. But the results of the regression analyses must be regarded as satisfactory when account is taken of the many factors that must contribute to variability in the results and which were not identified and measured.

Relevance of the results to practical problems

Kemper and Koch (1966) studied 519 soils from Western USA and Canada but used only one criterion of structural stability—the percentage of the soil retained on a sieve with 0·25 mm square openings when agitated under water in a standard way. (A correction was made for sand particles larger than 0·25 mm.) Aggregate stability was related to organic matter, clay, free iron oxide, and exchangeable sodium (the last was 'of little importance in the soils studied'). A regression equation involving all these factors accounted for 31% of total variance of aggregate stability. The most consistent correlation was with organic matter: clay was important only in well-mixed surface soils; free iron oxide was important in stability of subsoils, but was less important in cultivated topsoils. Increasing organic matter to more than 2% added little to stability of soil aggregates but with less than 1% stability decreased rapidly.

Kemper and Koch reviewed the literature on aggregate stability in relation to soil structure. Wherever conditions are comparable, my results obtained on British soils fit those of Kemper and Koch and earlier workers. Large instability of pore space on water slaking is the reverse of large aggregate stability; measurements of both show the importance of organic matter content, but my work also shows that the amount of gravel + coarse sand + fine sand is even more important than organic matter in arable soils. The aggregates usually stable in wet sieving tests are much smaller units of the structure than the assembly of crumbs and other particles that make up cultivated land

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TABLE 14

Comparisons of variance associated with regressions of soil physical tests upon soil composition involving one, two or more independent variates

	% Variance accounted for		
	Arable soils	Grassland soils	All soils
Bulk density (BD)			
%N	38	56	48
%OC	34	69	49
%N, % Clay	38	61	49
%CP, %OC, (%CP)²	39	(72)	52
% Clay, Log %OC, (% Clay)²	(36)	85	(48)
%CP, Log %OC, (%CP)²	40	(79)	50
Water holding capacity (WHC)			
%N	44	80	58
%N, %OC	53	(74)	62
%CP, %OC, (%CP)²	57	(73)	64
% Clay, Log %N	50	86	57
Water slaking instability (I/WS)			
%CP	64	23	51
%N	45	28	46
%CP, %OC	71	(28)	61
%CP, %OC, (%CP)²	73	45	64
%CP, %N, Log %CP	71	46	63
%CP, %OC, (%CP)², (%OC)²	(73)	(49)	67
Dry slaking instability (I/DS)			
%CP	69	65	61
%CP, %OC	(70)	69	(62)
%CP, Log %CP	73	69	64
%CP, %OC, (%CP)²	76	(71)	(66)
Total mechanical slaking (I/MS)			
%CP	32	36	33
%N	19	73	39
%CP, %OC	35	(66)	48
%CP, %OC, (%OC)²	(35)	(66)	49
Breaking strength (BS)			
%CP	53	11	37
%Clay	48	35	39
%CP, %OC	67	57	63
%CP, %N	65	67	62
%CP, %OC, (%OC)²	(67)	62	64
%CP, Log %N	63	67	59

CP = % Coarse particles (6–0·02 mm)
OC = % Organic carbon (Walkley & Black)
N = % Total N
Clay = % Clay (< 0·002 mm)
( ) = Regression not significant

usually described as having good tilth. They are also much smaller than the structural units in subsoils. Aggregates that are very stable in water usually have 'skins' of clay, or are cemented by iron oxides or organic matter. For these reasons, Kemper and Koch found that both organic matter and iron oxide had greater power to bind aggregates in subsoils than in cultivated surface soils. Aggregates in sub-surface layers result from pedogenic processes, whereas aggregates in cultivated topsoils largely depend on farming systems and cultivations and their stability depends greatly on both clay content and organic matter. Therefore a subsoil may contain a larger proportion of aggregates stable to wet sieving, provided the processes that developed it encouraged the subsoil to accumulate organic matter and to form stable ferric oxide bridges and cements binding particles

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together. This, of course, implies that the plant community under which the soil developed was deep rooting (to provide organic residues) and that the soil was well drained (to permit both deep rooting and the aerobic conditions in which ferric oxides are stable).

The aggregates that are stable to wet sieving are probably permanent units of the soil structure and may be of more direct use in pedological investigations than in planning arable farming. The aggregates used in this work are much more closely related to the assembly of particles that make up the structure and tilth thought important for crop growth. They are transitory and are formed when the weakest mechanical links in larger soil structures are broken by the forces exerted by freezing, by wetting and drying, or by cultivations. The best measure of structure that affects crop production is probably the amount of stable pore space expressed by capacity to hold water in the field; with this definition good structure implies an assembly of small, medium and large pores that, while permitting rapid drainage, nevertheless holds much water at relatively low tension.

The tests used were devised to assess soil characteristics important in planning land use, especially for arable farming and they are commended to investigators who advise farmers; they should also be useful measurements for making practical use of soil surveys. The methods are empirical, but so then are the conditions chosen for wet sieving tests of aggregate stability. Bulk densities and laboratory assessments of water holding capacities are easily measured; they are basic properties of the soils. The other tests were 'purpose designed'. Wet slaking shows whether soils will retain the good tilth established by suitable cultivation during spring or whether the structure collapses to a mass of soil with no macrostructure and having minimum pore space when saturated with water. Dry slaking shows how easily soil could be damaged by cultivations when it is dry enough to carry tractors. Total slaking shows the soil properties that make for resistance, or the lack of it, to compression by tractors and other implements used when soil is saturated with water. Compression caused by ploughing, or cultivating wet soil, or by traffic, is remedied when clods are easily broken; the 'breaking strength' test examines this possibility.

The results of all the tests are related to easily measured soil properties and are associated with mechanical analyses and organic matter contents by the simple equations listed. These may be used confidently to extend this work to other British soils and as an aid in forecasting behaviour when soils are cultivated. Reasons for having confidence in the relationships established are the close agreements between averages of measured properties and average values calculated from equations, and by the large percentage of the total variance accounted for in many of the regressions. When the soils used by Kemper and Koch were divided into 'surface cultivated layers', 'surface sod layers' and 'subsurface layers', regressions involving organic matter, clay and ferric oxide, accounted for 44, 35 and 38 % respectively of the variance in aggregate stability. By contrast, several of the properties measured here were much more closely related to soil composition; it was common for 60 % or more of the variance to be accounted for and some equations increased this to 75 or 80 %.

The 'structure' of soils that affects crop growth has never been satisfactorily defined and it is improbable that any single laboratory test, or group of tests, can be devised to do so. Crop growth is altered both by pore space arrangements in topsoil and by the subsoil characteristics that govern drainage and root penetration. Ability to drain speedily so that aerobic conditions are quickly re-established after rain, together with capacity to retain much water at low tension, are probably the most important soil characters affecting yields in Britain. Arrangements of pores, cracks and channels that remove water

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quickly, also permit deep rooting and ensure that roots are not killed by water-logging. These conditions may also favour development of ferric oxide cements that bind particles into the kinds of aggregates found stable in wet sieving tests. A more complete assessment of the suitability of land for modern arable farming may be obtained by using the tests described here to assess top soil behaviour and a wet sieving test to assess the structure of subsoils.

Kemper and Koch (1966) showed the large effect that organic matter has on stability of aggregates in sub-surface layers, with improvements continuing up to 4% organic matter (few British subsoils in well-drained land have as much as 2%). The effects of free Fe_2O_3 were even more striking, with percentage aggregate stability increasing from 64% to 94% as free Fe_2O_3 increased from barely measurable to 2·5%; Fe_2O_3 cements had much more effect on stability of subsoils than of surface cultivated layers. It may be profitable to apply these concepts to assessing structure of British soil profiles. For example Broadbalk subsoil is stable and drains well. Kemper and Koch found this equation measured % stable aggregates in sub-surface layers.

$$AS = 65{\cdot}6 + 32{\cdot}8 \log \%\,OM - 0{\cdot}05\,\%\,clay + 0{\cdot}008\,\%\,(clay)^2 + 6\,\%\,Fe_2O_3$$

Applying this formula to values given by Avery and Bullock (1969) for Broadbalk subsoil 48–70 cm deep, suggested 84% of the aggregates were water stable. This value considerably exceeds the average aggregate stability (76%) of all the subsoils investigated by Kemper and Koch.

Summary and conclusions

Aggregates of 4–6 mm, prepared from 189 soils (mainly British) by deep freezing, thawing and air drying, were used in physical tests to relate soil composition with the instability of soil aggregates to water slaking, dry mechanical slaking and to combined wet and dry mechanical slaking. Breaking strength of compacted soil cylinders, bulk density and water holding capacity were also measured. There were 147 arable soils and 37 from grassland.

The water slaking test measured the stability of soil particles to capillary forces caused by water entering pores within air dried aggregates, and to the strains set up by hydration and swelling of clay and organic matter. Slaking was most influenced by content of coarse (6–0·02 mm) particles in soils containing less than 2% organic carbon. With more than 2% organic carbon (or 0·25% total nitrogen) the form of organic matter was important; grassland soils were more stable than arable soils, whose stability was little affected by organic manures. Soils with more than 70% coarse particles (6–0·02 mm) were very unstable, lacking clay and silt to bind the larger particles.

The dry slaking test measured the stability of air-dried soil particles to mechanical crushing. The results depended even more than those with water slaking on the amount of coarse mineral particles in the soil. The organic fraction of soil had much less effect and arable and grassland soils did not differ greatly. Organic manuring did not make soils more stable.

Total mechanical slaking measured the effect of mechanical compaction on soil that had been water slaked and then drained. The proportions of coarse mineral particles (6–0·02 mm) were most closely related to results of this test; clay, silt and coarse organic matter contents were not well related. Grassland soils were more resistant than arable

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soils to total slaking; %N was the best measure of their organic matter content for indicating stability.

Breaking strength measured the cohesion between particles of dried soil in a section of a cylinder formed by mechanical slaking when wet; this was air-dried before the test. The strength of the soil cylinders was more closely correlated with coarse particles (6–0·02 mm), and with % clay content, than with any of the measurements of organic matter. Both clay and silt contents were more closely related with breaking strength of cylinders from arable soils than from grassland.

Bulk density measured on <2 mm soil was more closely related to organic carbon (or nitrogen) contents, especially of grassland soils, than to coarse particles, clay or silt. The amount of 'coarse' organic matter, mostly undecomposed plant remains, was related to bulk density especially of grassland soils.

Water holding capacity of <2 mm soil was also more closely related to organic matter contents, especially of grassland soils, than to sand, silt, or clay fractions.

The soils used differed considerably in calcium carbonate contents, but there was no detectable association between this fraction and the physical properties measured.

The apparatus used was simple enough for routine measurements on soils; it could be further mechanised and the ancillary chemical analyses automated.

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The chemical composition of water from land drains at Saxmundham and Woburn, and the influence of rainfall upon nutrient losses

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Introduction

Most of the work on the composition of drainage done since Lawes, Gilbert and Warington (1882) published their classic account of the drainage from the Broadbalk Wheat Experiment, has been concerned with drainage from soil columns and boxes, or from filled lysimeters, in which conditions are rarely comparable to those in the field. Work with lysimeters constructed around undisturbed soil blocks are more relevant to field drainage, but they may leak or water may flow through fissures made in constructing the lysimeter or between its wall and the soil. Examples in the United Kingdom of work with soil block lysimeters are at Rothamsted (Lawes & Gilbert, 1881; Miller, 1906) and at Craibstone, near Aberdeen (Hendrick, 1930; Hendrick & Welsh, 1938). The composition of drainage from farmland on different soil types has been little studied. In their work at Rothamsted, Lawes, Gilbert and Warington (1882) used the drainage system installed on Broadbalk field in 1849 to measure the losses of plant nutrients from experimental plots under continuous wheat. Work done in other countries has been comprehensively listed by S. F. Atkins (1970) and by the Tennessee Valley Authority (1969). Both publications emphasise losses of nitrate from agricultural land. Comprehensive work on composition of drainage has been done recently in irrigated areas of U.S.A. (Johnston *et al.*, 1965). Wadleigh (1968), who reviewed recent work on losses of nutrients from agricultural sources, concluded that nitrate in well waters came mainly from the natural nitrification in soils and from the nitrification of human and animal sewage; he found no clear evidence that using fertiliser resulted directly in large nitrate concentrations. Losses of nitrogen and phosphorus from agricultural land in Britain were discussed by Cooke and Williams (1970) at a Symposium of the Society for Water Treatment and Examination, where Owen (1970) reported on the composition of land drainage in the Ouse Valley, and Tomlinson (1970) described changes in nitrate in river water in relation to changes in the fertilisers used in the catchment areas concerned.

The measurements now to be described were on two different soils, 100 miles apart, having contrasted drainage systems, but both given current dressings of fertiliser. The influence of soil type on the chemical composition and volume of drainage water is discussed. The results, thought to be unique for modern conditions in England, are relevant to eutrophication of natural waters, and to all work intended to make fertilisers more efficient.

The chemical compositions and flowrates of drainage water at Woburn and Saxmundham Experimental Stations were measured from March 1968 until March 1970. At Woburn, the drainage was sampled twice a month; at Saxmundham, where drainage flows varied more, sampling was more frequent, especially during very wet periods in spring and autumn when losses of nutrients, especially nitrogen, were most. Figure 1 shows the positions and numbers of the drains at the two sites. Methods of sampling and estimating flows, and analytical methods, are briefly described in the Appendix.

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Saxmundham. The Experimental Station at Saxmundham, started in 1898, is now only one field (Harwood's about 3 ha) surrounded by deep ditches. Animals are not kept and no drainage from higher land reaches the field; nutrients come solely from rain, soil and fertilisers. The main ditch runs down a shallow valley and intermittently becomes a small stream; water finally flows into the River Alde. The positions and outfalls of the drains known to have been installed in 1948 are in Fig. 1; records of an older drainage system on Harwood's field were lost in a fire. Drain 4, which flows intermittently, is part of this old system. The modern drains are thought to be at least 65 cm below the surface. The field was mole-drained 56 cm deep during the dry autumn of 1964.

The Saxmundham soil is derived from calcareous boulder clay with rather more sand than is common for this. It is classified as Beccles Series. The surface soil slakes and caps easily; the subsoil is mostly impervious compact clay, interspersed with lenses of lighter-textured material. Deep trenches excavated 500 m away for gas mains suggest that the sandy lenses may be widespread. The drains have outfalls 1·2 to 1·5 m below the surface and discharge into the deep ditches surrounding the field. In addition to water from the land drains, surface water from the field was analysed, as also was water from a pond behind Spark's barn to the south of Harwood's Field; the pond is filled by land drainage and in most seasons there is no flow from it. Drain 6 discharged from the adjacent West Field (which has similar soil but is imperfectly drained); it was sampled because the composition of the water differed considerably from that drained from Harwood's Field.

Woburn. The drains differ from those at Saxmundham. Crawley Mill Farm is 1·5 to 3 km north-east of Woburn, mostly on the edge of the Lower Greensand ridge and down-wash from it. The lower part is heavy Drift deposits overlying Oxford Clay. All the water drains northward to the Ouzel. The land is irregularly drained, by drains of uncertain age and extent that must have been put in for local need and not to any general pattern. Drains 1, 2 and 3 run from deep soil profiles of lighter drift overlying relatively impervious resorted Oxford Clay; they flow continuously through the year. Drain 4 collects water from an area of resorted Oxford Clay under permanent grass that is periodically grazed. Its flow is much less than those of the other drains and there is little or none during dry weather. Drains 5 and 6 both originate in a spring at the rear of Honeypot Field; No. 5 discharges into a nearby ditch, Drain 6 traverses shallowly a cattle watering point in an adjacent field. Differences in composition of water from these two drains reflects pollution in Drain 6. The small stream (No. 7) comes from an underground source, provided with soil traps, in Mill Dam Close. It flows behind the farm buildings, joins the stream to the north of Long Mead and ultimately discharges into the River Ouzel. It was sampled north of the farm buildings where the flow was measured at a small weir. This stream flowed continuously throughout the two years, and diminished only in very dry weather. The artificial lake south of the farm buildings, which was sampled as a static source, discharges by a drain to the stream and its composition was an interesting comparison with that of the water from Drain 1 which fed it. Figure 1 shows the extent and nature of the types of soil in the drained areas of the farm.

Effects of weather on drainage

Tables 2 and 3 show the amount and intensity of rainfall, soil temperature and drainage, and the mean combined flow of the drains at each site. Table 1 gives the means and ranges of the flowrates of individual drains. For Saxmundham, the total monthly drainage flow is also expressed as a percentage of the monthly rain, as the drains serve a finite area.

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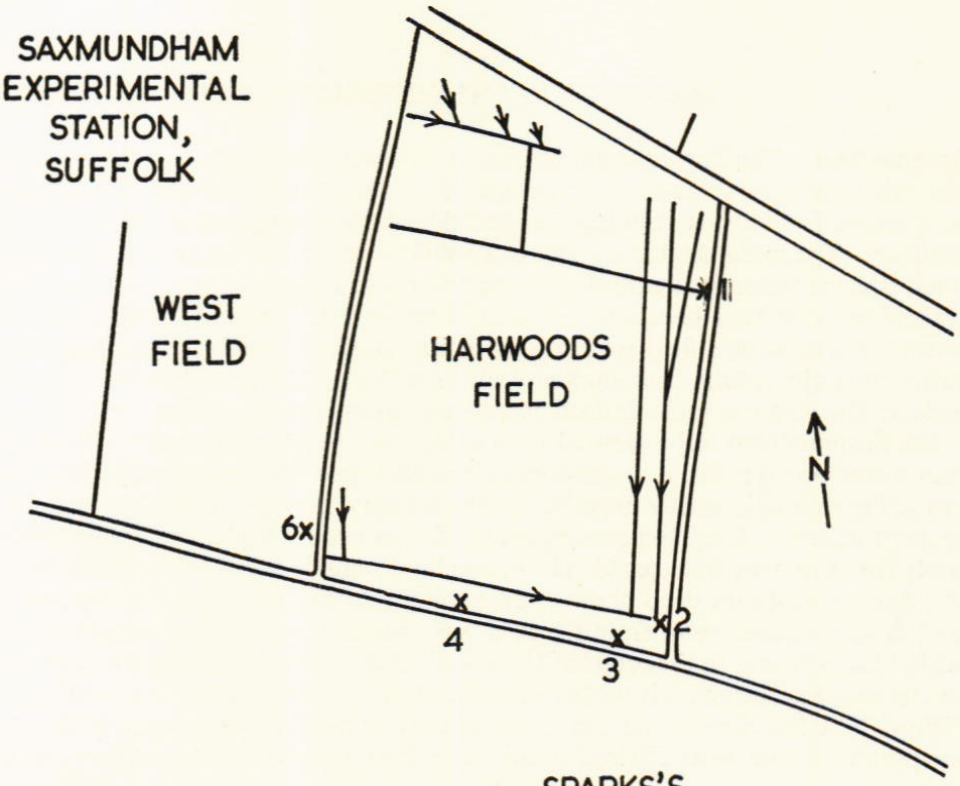

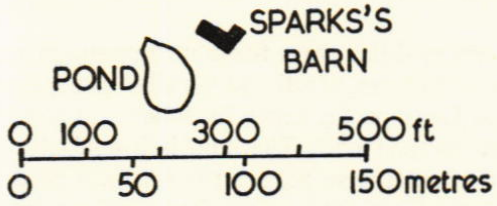

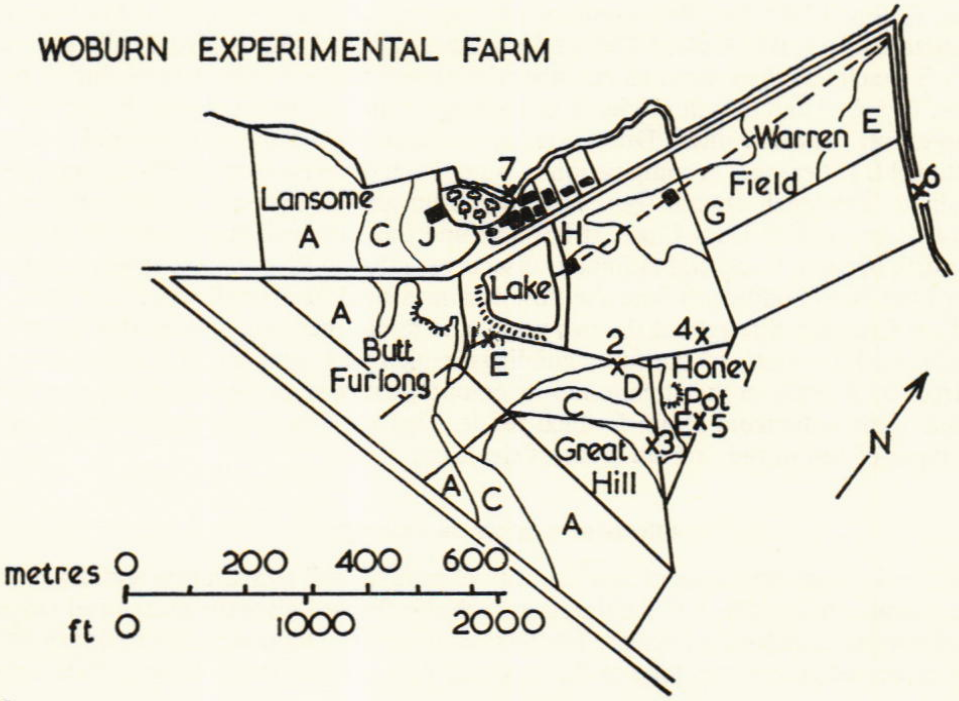

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At Woburn the catchment areas are not known and a similar calculation cannot be made.

Mean flowrates were greater at Woburn than at Saxmundham but varied less. At Saxmundham very large flowrates were recorded for short periods, but often the drains ran very little or not at all. The flow from Drain 6 (West Field) was most erratic, especially during the second year; although the drainage system in West Field is recent, it works badly, and the field is often waterlogged with much surface run-off during heavy rain.

Saxmundham. The mean flow from Drains 1–4 at Saxmundham was much greater during the second (16 l/min) than the first year (9·4 l/min). The mean monthly flow-rates also differed during these two years, with flows much larger in the first three months and the last five months of the second year, when September and October were dry. The drainage flow pattern followed the rainfall distribution in both years, the beginning and end of the 1969–70 period was much wetter with a larger proportion of the rain in increments >10 mm daily. There was only 9 mm of rain during September and October 1969, whereas in these months in 1968 nearly 190 mm of rain fell, much of it in increments >10 mm daily. The soil, 30 cm deep, was colder from March to June 1969 than in 1968 but was warmer for the succeeding three months, when evaporation was greater. In November 1969, after two dry months, nearly 60 mm of rain was needed to start drainage; total soil moisture in the 0 to 23 cm horizon was then 20% v/v and 30% v/v 45–92 cm deep. Estimations of the moisture deficit at these two depths by the end of September, together with the observed volume of drainage during November, suggested that, when rainfall at Saxmundham is largely in increments >10 mm daily, the subsoil below plough depth does not take up the extra water and prevent rapid drainage, so there are losses of soluble nutrients, especially N. This is one feature of the considerable difference in behaviour between the Saxmundham and Rothamsted soils; at Rothamsted roots penetrate deeper, which improves subsoil condition and permits plants to use more subsoil moisture. Of the relationships between mean monthly flow-rates, total monthly rain, rain >10 mm weekly, rain >10 mm daily, or >2·5 daily, the closest was between flow rate and rain >10 mm weekly, especially during the winter (September–February). Rainfall intensities and drainage were less well related during summer (March–August) because of the greater evaporation during these months. As mean annual concentrations of nutrients in drainage at Saxmundham fluctuated less than mean annual flowrate, flowrate dominated the quantities lost in drainage each year.

Woburn. Rainfall during March, April and May of 1969 was more than in 1968 but drainage flowrates were similar in both years. Heavy rain from June–September 1968 maintained larger flow than in 1969 when the monthly rainfall was much less. The dry months of September and October 1969, when only 15 mm of rain fell, contrasted sharply with the 149 mm that fell during the comparable period in 1968. The flows from the land

Fig. 1. Plans of Saxmundham and Woburn (see opposite page). Drain outfalls numbered.

Key to the soil types at Woburn.

A. Brown earths on resorted Lower Greensand.

C., D., E. Gley soils
- On colluvial Lower Greensand/Oxford clay.
- On reworked Lower Greensand and Oxford clay.
- On resorted Oxford clay.

G., H., J. Alluvial complexes
- Heavy.
- Light.
- Undifferentiated and made ground.

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TABLE 1

Rates of flow from individual drains at Saxmundham and Woburn. Averages for the two periods (l/min)

	Woburn, 1968–69					Saxmundham, 1968–69		
Drain	Mean	Max.	Min.		Drain	Mean	Max.	Min.
1	13·4	22·5	8·7	1	Harwood's Field	3·1	80·0	0·0
2	10·1	25·0	1·7	2		3·9	80·0	0·0
3	3·3	15·0	1·0	3		1·7	20·0	0·0
4	1·9	8·7	0·12	4		0·7	60·0	0·0
5	3·6	15·0	0·62					
6	5·5	15·0	1·7	6	West Field	0·9	60·0	0·0
Stream	130·0	130·0	130·0					
	1969–70					1969–70		
Drain					Drain			
1	9·0	22·5	1·0	1	Harwood's Field	4·9	60·0	0·0
2	2·3	2·5	1·0	2		7·6	120·0	0·0
3	2·8	15·0	0·25	3		2·0	80·0	0·0
4	1·1	8·7	0·0	4		1·4	50·0	0·0
5	3·3	15·0	0·25					
6	18·3	80·0	2·5	6	West Field	1·1	15·0	0·0
Stream	75·0	130·0	15·0					

TABLE 3

Relationships between rainfall, its intensity, soil temperature, and drainage at Woburn

		Rainfall (mm)				Flowrate (l/min)	
Year	Month	Total	>10 mm daily	Rainy days (>0·25 mm)	Soil temperature 30 cm (°C)	Drains 1–6	Spring
		22 March 1968–10 March 1969					
1968	March	5	0	4	7·0	8·2	—
	April	51	11	13	8·1	6·7	—
	May	55	15	17	10·9	4·8	130
	June	78	37	15	15·3	3·5	130
	July	109	77	13	16·6	3·3	130
	August	75	34	14	15·9	3·7	130
	September	108	66	19	15·0	4·2	130
	October	41	12	13	13·1	4·1	130
	November	53	20	15	10·3	5·5	130
	December	47	12	12	4·8	9·1	130
1969	January	76	11	22	4·5	11·8	130
	February	57	22	15	2·1	12·1	130
	March	4	0	1	2·2	6·4	130
Total		759	317	173	—	—	—
Mean		—	—	—	9·7	6·4	130
		11 March 1969–23 March 1970					
1969	March	52	34	12	3·8	—	—
	April	34	14	15	7·2	6·3	130
	May	75	28	17	11·9	5·3	130
	June	30	14	10	14·9	4·1	130
	July	40	13	7	17·6	4·5	130
	August	60	24	14	17·0	4·0	130
	September	12	0	9	15·1	3·7	80
	October	3	0	4	12·9	3·2	15
	November	65	18	15	7·8	2·1	15
	December	49	0	18	4·6	8·2	30
1970	January	56	11	22	4·2	6·0	15
	February	57	0	20	3·4	25·7	80
	March	50	12	13	3·3	6·9	15
Total		583	168	176	—	—	—
Mean		—	—	—	9·5	6·7	75·0

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TABLE 2

Relationships between rainfall and its intensity, evaporation, soil temperature and drainage at Saxmundham

Year	Month	Rainfall: Total (mm)	Rainfall: Daily >10 mm	Evaporation Eo (mm)	Soil temperature at 30 cm depth (°C)	Drainage: Drains 1–4: Observations (days)	Drainage: Drains 1–4: Flowrate (l/min)	Drainage: Drains 1–4: Total (as % of rain)	Drainage: West Field Flowrate (l/min)
21 March 1968–11 March 1969									
1968	March	7	0	—	5·1	9	1·0	6·5	0·3
	April	27	0	87	8·3	21	0·1	0·5	0·0
	May	42	18	64	11·4	27	2·5	7·8	0·0
	June	56	10	93	16·1	27	0·1	0·3	0·0
	July	64	17	84	16·8	27	0·2	0·4	0·0
	August	73	33	76	16·3	28	1·0	1·9	0·0
	September	138	106	62	14·8	24	46·5	38·4	1·2
	October	51	11	28	12·5	27	8·2	20·9	0·2
	November	41	0	—	8·0	26	11·9	36·3	1·9
	December	45	27	—	4·8	22	13·2	30·9	3·5
1969	January	49	0	—	4·8	27	22·9	59·4	2·7
	February	73	25	—	2·5	24	12·5	19·6	1·3
	March	12	0	—	3·7	9	2·4	8·2	0·3
Total		678	247	—	—	298	—	—	—
Mean		—	—	—	9·6	—	9·4	17·8	0·9
12 March 1969–16 March 1970									
1969	March	43	19	—	3·7	17	29·7	55·9	1·3
	April	36	0	55	7·3	25	2·4	7·9	0·4
	May	92	46	83	11·7	27	24·3	34·0	0·9
	June	39	13	100	15·1	24	1·9	5·4	0·1
	July	99	98	119	19·0	23	5·5	6·0	0·0
	August	73	42	82	16·7	27	8·5	14·9	0·2
	September	2	0	62	15·5	27	0·0	0·0	0·0
	October	7	0	33	13·0	27	0·0	0·0	0·0
	November	99	73	—	7·1	27	15·7	20·3	0·5
	December	76	33	—	3·7	21	31·4	41·3	2·8
1970	January	71	13	—	4·2	24	36·2	57·9	3·0
	February	55	11	—	2·8	17	28·7	41·9	4·4
	March	23	0	—	3·8	13	24·2	24·7	0·9
Total		715	348	—	—	299	—	—	—
Mean		—	—	—	9·5	—	16·0	23·9	1·1

TABLE 4(a)

Concentrations of NH_4–N, NO_3–N, PO_4–P, SO_4–S and Cl (mg/l) in drainage water from Harwood's Field, Saxmundham, from 21 March 1968 to 11 March 1969 and from 12 March 1969 to 16 March 1970, averaging values from drains 1–4

		NH_4–N			NO_3–N			PO_4–P			SO_4–S			Cl		
		Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
1968	March	0·21	0·90		6·1	8·2	4·0	0·06	0·70		116	153	90	55	72	42
	April	0·22	1·40		6·4	10·7	3·7	0·07	0·15		143	176	107	54	71	47
	May	0·01	0·15		41·9	91·5	9·7	0·06	0·25		66	136	34	59	71	48
	June	0·22	0·60		25·5	30·0	19·3	0·00	0·00		47	55	34	34	43	22
	July	0·00	0·00		41·7	56·5	29·8	0·00	0·00		66	84	51	46	54	36
	August	0·00	0·00		14·3	49·1	4·9	0·05	0·20		36	67	21	38	52	27
	September	0·25	2·40	0·00	12·3	29·5	4·3	0·07	0·18	0·00	31	70	7	41	60	24
	October	0·09	0·40		7·8	11·0	5·8	0·00	0·00		39	61	23	46	55	36
	November	0·00	0·00		10·6	16·1	7·7	0·00	0·00		53	67	43	63	113	53
	December	0·00	0·00		10·7	13·3	7·4	0·06	0·20		52	70	39	59	67	50
1969	January	0·00	0·00		10·2	14·2	7·0	0·17	0·17		28	49	11	38	50	27
	February	0·00	0·00		5·8	8·1	4·2	0·00	0·00		46	79	17	40	73	16
	March	0·05	0·30		6·9	14·5	5·3	0·00	0·00		81	130	65	52	75	35
Mean 1968–69		0·08	0·47	0·00	15·4	27·1	8·7	0·04	0·14	0·00	62	92	42	48	66	36
1969	March	0·09	1·45		10·9	25·6	5·5	0·04	0·30	0·00	40	95	15	46	81	34
	April	0·06	1·20		10·0	27·5	5·5	0·00	0·00	0·00	96	114	80	58	80	43
	May	0·11	0·65		25·5	91·2	5·5	0·00	0·00	0·00	56	120	32	48	78	27
	June	0·01	0·20		12·6	31·0	6·1	0·40	0·40	0·40	89	127	50	58	62	54
	July	0·00	0·00		6·2	22·6	2·4	0·00	0·00	0·00	26	28	24	32	31	20
	August	0·08	0·50		4·5	7·5	0·5	0·00	0·00	0·00	29	30	25	36	41	32
	September	—	—	0·00	—	—	—	—	—	—	—	—	—	—	—	—
	October	—	—		—	—	—	—	—	—	—	—	—	—	—	—
	November	0·00	0·00		26·9	40·3	13·0	0·11	1·20	0·00	63	72	50	102	129	62
	December	0·55	2·40		13·7	18·7	8·0	0·09	0·30	0·00	54	104	30	43	33	26
1970	January	0·34	2·30		8·6	10·6	0·0	0·00	0·00	0·00	51	57	46	30	49	22
	February	0·12	1·50		7·8	9·7	6·1	0·00	0·05	0·00	43	76	29	23	40	17
	March	0·43	3·00		7·7	9·6	6·0	0·00	0·00	0·00	60	70	54	38	56	28
Mean 1969–70		0·16	1·20	0·00	12·2	26·7	5·3	0·06	0·20	0·04	55	81	40	47	62	33

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TABLE 4(b)

Concentrations of cations (mg/l) in drainage water from Harwood's Field, Saxmundham, from 21 March 1968 to 11 March 1969 and from 12 March 1969 to 16 March 1970, average values from drains 1–4

		Ca			Mg			K			Na		
		Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
1968	March	222	256	192	14·9	23·0	9·8	1·8	4·4	0·4	30·4	38·0	24·0
	April	246	270	212	19·9	27·5	12·6	1·5	3·9	0·6	35·4	41·0	31·0
	May	245	280	215	11·2	16·8	8·5	1·2	2·6	0·5	24·0	28·0	18·5
	June	197	237	150	7·7	9·2	6·3	1·8	2·6	1·0	18·9	22·0	15·0
	July	246	277	218	9·6	12·7	7·4	1·2	1·6	1·0	23·5	30·0	19·2
	August	197	245	128	6·4	10·0	3·7	1·9	3·9	0·6	16·2	23·5	9·4
	September	152	225	84	5·6	12·7	3·0	1·8	4·8	0·8	16·0	36·0	10·8
	October	174	222	105	7·1	12·9	3·8	1·9	3·4	1·0	18·3	23·5	11·6
	November	165	204	116	8·2	9·9	5·7	1·3	2·7	0·7	18·3	22·0	15·0
	December	155	168	137	8·5	10·6	6·2	1·3	3·6	0·6	21·6	28·0	15·6
1969	January	133	163	108	4·7	8·9	4·1	1·5	2·2	1·0	14·6	18·0	11·6
	February	156	232	62	7·7	7·1	2·7	0·9	1·7	0·4	17·8	29·2	7·4
	March	210	244	194	12·6	21·4	9·5	0·7	1·2	0·5	26·2	32·4	17·4
Mean 1968–69		192	232	148	9·5	14·0	6·4	1·4	3·0	0·7	21·6	28·6	15·9
1969	March	151	222	114	7·7	18·3	4·2	1·5	3·3	0·6	19·8	44·8	12·0
	April	214	236	188	14·9	28·8	12·1	1·1	1·3	0·8	26·1	28·8	23·0
	May	195	260	144	8·9	16·1	4·5	1·7	4·2	0·6	18·9	31·2	11·0
	June	206	206	206	10·8	10·8	10·8	3·8	3·8	3·8	22·4	22·4	22·4
	July	111	124	98	4·2	4·6	3·9	1·5	2·9	1·0	13·0	14·2	12·0
	August	133	150	118	4·2	4·3	3·9	1·4	1·6	1·4	13·2	14·0	11·8
	September	—	—	—	—	—	—	—	—	—	—	—	—
	October	—	—	—	—	—	—	—	—	—	—	—	—
	November	210	236	160	7·2	9·3	4·7	2·6	5·2	1·6	17·2	20·8	12·6
	December	146	217	102	6·1	10·3	3·3	2·2	4·2	0·8	16·5	24·8	12·0
1970	January	175	270	166	4·3	14·0	0·8	1·1	1·4	0·8	15·6	20·8	12·8
	February	140	140	88	3·9	4·7	3·2	1·4	2·3	0·8	13·4	22·0	10·0
	March	163	176	148	7·9	8·7	7·3	1·7	3·1	0·7	21·1	24·0	19·2
Mean 1969–70		168	203	139	7·3	11·8	5·3	1·8	3·0	1·2	17·9	24·3	14·4

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drains diminished from September 1969 and their rates, and that of the stream, remained small until March 1970; the stream had a larger and constant flow throughout 1968. There was little association between rainfall >10 mm daily and drainage flowrates, which depended more on longer periods of dry or wet weather. This is because the soil profiles are much deeper and the areas drained much larger than at Saxmundham. The large flowrate from Drain 6 during February 1969 is not readily explained, but it is a shallow drain and may have gathered some surface water. Drain 5, which originated nearby, also had a large flowrate during this month. The larger mean annual flowrate for 1968–69, especially of the stream, is the cause of larger estimated losses of nutrients than during 1969–70.

The contrasts between the drains at Woburn and at Saxmundham (other than No. 4, which has its source in resorted Oxford Clay and resembles the Saxmundham drains), are: (1) that flowrates from Woburn drains were less affected by daily rainfall; (2) the concentrations of nutrients did not show the sharp maxima, especially of NH_4/N, NO_3/N and K, found in drainage water at Saxmundham during early spring and summer.

The effects of rainfall and volume of drainage on composition of the water

Tables 4a and b give the monthly means and ranges of concentrations of nutrients in drainage water at Saxmundham during 1968–70. Table 5 shows the relationships between the individual drains, expressed as mean annual concentrations of ions, together with values for pH and specific conductivity. Tables 6a, b and 7 give the corresponding measurements from the sources examined at Woburn. Of the major plant nutrients, nitrogen is

TABLE 5

Average concentrations of ions (mg/l), conductivities, and pH values in water from five drains and one static source at Saxmundham 1968–69 and 1969–70

		Harwood's Field				West Field	
		Drain 1	Drain 2	Drain 3	Drain 4	Drain 6	Pond
Calcium	1968–69	190	190	201	155	124	133
	1969–70	175	152	161	153	120	124
Magnesium	1968–69	8·9	9·8	10·9	6·0	7·7	10·3
	1969–70	6·9	7·2	7·6	5·2	7·7	10·6
Potassium	1968–69	1·9	1·2	1·1	1·9	2·0	17·7
	1969–70	2·2	1·6	1·4	1·5	2·1	18·9
Sodium	1968–69	23	22	22	15	15	29
	1969–70	20	17	18	13	13	29
Ammonium-N	1968–69	0·13	0·06	0·05	0·03	0·09	1·43
	1969–70	0·18	0·17	0·17	0·13	0·28	1·47
Nitrate-N	1968–69	11·5	12·7	18·7	15·9	2·5	0·6
	1969–70	12·0	10·9	12·4	14·9	5·4	0·8
Phosphorus	1968–69	0·06	0·02	0·04	0·08	0·13	0·58
	1969–70	0·08	0·02	0·01	0·04	0·00	0·44
Sulphate-S	1968–69	57	67	65	33	35	18
	1969–70	52	52	64	37	46	22
Chloride	1968–69	55	44	46	52	33	63
	1969–70	59	43	41	38	30	63
Conductivity (μ mhos/cm)	1968–69	950	940	1000	760	650	800
	1969–70	940	850	870	720	650	790
pH	1968–69	7·6	7·6	7·7	7·7	7·6	7·7
	1969–70	7·8	7·7	7·8	8·0	7·8	7·9

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TABLE 6(a

Concentrations of NH_4–N, NO_3–N, PO_4–P, SO_4–S and Cl (mg/l) in drainage water from Woburn, from 22 March 1968 to 10 March 1969 and from 12 March 1969 to 16 March 1970; average values from drains 1–6

		NH_4–N			NO_3–N			PO_4–P			SO_4–S			Cl		
		Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
1968	March	0·00	—	—	12·0	—	—	0·14	—	—	—	—	—	29·5	—	—
	April	0·00	—	—	11·1	—	—	0·14	—	—	69·9	—	—	37·1	—	—
	May	0·02	0·30	0·00	11·2	21·9	1·2	0·15	0·55	0·00	61·4	130·6	36·0	32·7	55·0	12·2
	June	0·53	3·20	0·00	15·6	23·7	1·8	0·37	0·75	0·00	53·8	87·8	37·7	44·4	126·0	16·0
	July	0·03	0·30	0·00	11·8	24·8	2·0	0·15	0·63	0·00	55·5	105·0	32·7	28·8	54·5	13·0
	August	0·00	0·00	0·00	12·0	24·7	1·2	0·18	0·53	0·00	48·7	130·0	23·0	26·9	45·5	11·3
	September	0·00	0·00	0·00	12·7	25·6	2·0	0·14	0·53	0·00	47·8	121·0	16·5	27·0	47·5	11·8
	October	0·00	0·00	0·00	11·0	25·2	1·2	0·16	0·65	0·00	32·9	78·5	15·0	27·3	47·5	11·5
	November	0·00	0·00	0·00	12·8	26·2	1·9	0·14	0·52	0·00	54·8	119·0	30·8	27·0	45·5	12·5
	December	0·04	0·50	0·00	12·2	25·5	1·5	0·11	0·50	0·00	61·5	117·0	32·0	30·2	51·5	12·5
1969	January	0·00	0·00	0·00	13·7	23·8	4·8	0·22	0·85	0·00	55·3	102·0	23·0	30·2	55·0	14·5
	February	0·00	0·00	0·00	12·1	20·0	6·5	0·08	0·45	0·00	51·3	99·5	28·0	29·2	51·0	17·0
	March	0·26	—	—	—	—	—	0·00	—	—	56·4	—	—	27·7	—	—
Mean 1968–69		0·07	0·43	0·00	12·3	24·1	2·4	0·15	0·60	0·00	54·1	109·0	27·5	30·6	57·9	13·2
1969	March	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	April	0·00	0·00	0·00	13·3	22·0	7·5	0·16	0·50	0·00	51·4	84·7	35·3	26·8	40·0	16·0
	May	0·01	0·15	0·00	12·3	21·0	4·5	0·06	0·50	0·00	52·0	108·0	30·8	26·1	42·5	14·2
	June	0·07	0·80	0·00	12·9	24·0	4·5	0·17	0·50	0·00	48·5	107·8	33·0	26·0	42·0	13·0
	July	0·03	0·20	0·00	14·5	24·3	4·5	0·19	0·55	0·00	50·7	103·5	37·0	35·3	126·0	14·5
	August	0·00	0·00	0·00	12·8	24·0	2·4	0·10	0·50	0·00	56·4	136·0	35·5	31·2	64·5	12·5
	September	0·00	0·00	0·00	14·7	25·3	3·5	0·12	0·40	0·00	45·0	59·5	39·0	24·0	40·0	14·0
	October	0·02	0·10	0·00	16·4	26·2	5·9	0·26	0·60	0·00	44·1	53·0	38·0	25·2	40·5	16·0
	November	0·23	0·60	0·00	16·4	26·0	4·5	0·19	0·40	0·00	57·5	141·0	37·5	34·5	81·0	12·0
	December	0·00	0·00	0·00	15·4	24·5	4·0	0·14	0·50	0·00	67·5	148·0	37·5	36·6	99·5	10·5
1970	January	0·00	0·00	0·00	13·8	25·0	3·0	0·06	0·40	0·00	70·9	163·0	41·0	29·2	47·0	12·5
	February	0·00	0·00	0·00	17·3	26·6	5·6	0·00	0·00	0·00	63·9	132·0	38·0	30·6	50·5	16·5
	March	0·00	0·00	0·00	17·4	32·2	8·6	0·00	0·00	0·00	62·3	132·0	36·5	29·6	44·0	18·0
Mean 1969–70		0·03	0·15	0·00	14·8	25·1	4·9	0·12	0·40	0·00	55·8	114·0	36·6	29·6	59·8	14·1

TABLE 6(b)

Concentrations of cations in drainage water from Woburn, from 22 March 1968 to 10 March 1969 and from 12 March 1969 to 16 March 1970; average values from drains 1–6

		Ca			Mg			K			Na		
		Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
1968	March	149	—	—	9·5	—	—	2·1	—	—	11·1	—	—
	April	167	—	—	10·8	—	—	5·8	—	—	12·8	—	—
	May	159	242	77	10·0	20·0	5·3	3·6	16·0	0·5	12·0	20·5	8·5
	June	129	231	44	7·9	10·9	4·8	12·9	64·0	0·6	11·5	15·6	9·4
	July	144	261	82	8·2	15·2	4·1	3·7	15·0	0·5	11·2	17·9	7·4
	August	151	333	41	9·6	18·5	5·2	3·2	9·6	0·5	11·0	18·0	8·3
	September	153	302	67	9·7	17·6	5·7	3·6	10·1	0·6	11·3	15·6	8·4
	October	163	288	75	9·2	17·0	5·2	3·5	13·6	0·6	10·9	15·0	8·0
	November	130	195	69	9·9	22·0	4·7	3·9	13·8	0·5	11·0	15·8	8·4
	December	144	177	55	9·3	18·0	5·0	4·2	13·6	0·4	10·8	15·2	8·0
1969	January	140	264	64	8·3	15·6	4·8	4·5	20·0	0·4	11·1	17·6	7·2
	February	147	242	65	9·0	18·0	5·0	4·0	18·0	0·4	11·1	18·4	8·0
	March	144	—	—	9·1	—	—	2·9	—	—	10·9	—	—
Mean 1968–69		148	253	64	9·3	17·3	5·0	4·4	19·4	0·5	11·3	17·0	8·2
1969	March	—	—	—	—	—	—	—	—	—	—	—	—
	April	128	182	69	9·7	17·8	5·1	2·9	5·8	0·5	10·6	15·4	8·0
	May	135	214	66	9·2	17·4	5·2	3·3	8·0	0·6	9·7	13·2	7·6
	June	134	220	69	9·5	19·8	5·1	3·4	9·6	0·6	10·7	16·0	8·4
	July	129	234	68	10·3	28·8	4·1	11·4	90·0	0·6	13·1	28·4	9·2
	August	129	232	72	9·8	25·2	4·3	7·5	31·0	0·6	12·6	26·4	8·8
	September	101	138	63	7·1	10·7	4·8	3·2	6·8	0·6	9·8	12·6	8·8
	October	106	136	64	7·1	10·7	4·9	3·4	6·7	0·6	9·7	12·4	8·6
	November	139	244	72	10·2	28·4	4·4	6·9	25·6	0·6	12·7	28·0	8·4
	December	137	256	67	10·7	34·0	3·3	7·8	40·8	0·8	12·0	26·4	7·2
1970	January	154	362	71	9·6	23·1	4·2	4·0	12·2	0·5	9·4	21·2	6·8
	February	147	256	86	7·8	15·3	4·3	4·9	19·2	0·6	10·8	18·0	7·4
	March	145	264	80	9·0	16·9	4·2	4·9	14·0	0·6	12·6	18·4	8·4
Mean 1969–70		132	228	70	9·2	20·7	4·5	5·3	22·5	0·6	11·1	19·7	8·1

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TABLE 7

Average concentrations of ions (mg/l), conductivities, and pH values of water from six drains, a permanent stream and one static source at Woburn, 1968–69 and 1969–70

		Drain 1	Drain 2	Drain 3	Drain 4	Drain 5	Drain 6	Stream	Lake
Calcium	1968–69	167	152	70	231	130	127	77	126
	1969–70	146	146	72	237	121	92	87	111
Magnesium	1968–69	9·5	6·8	10·3	16·7	5·2	7·0	8·6	11·3
	1969–70	8·4	6·2	9·9	21·3	4·6	5·8	8·7	10·5
Potassium	1968–69	1·9	0·7	4·4	15·7	0·6	3·4	3·7	8·6
	1969–70	2·2	0·6	4·7	19·2	0·7	5·3	4·7	9·0
Sodium	1968–69	14·3	9·7	8·7	16·1	8·7	10·1	11·6	15·5
	1969–70	13·3	8·9	8·9	19·4	8·4	9·3	11·6	15·8
Ammonium-N	1968–69	0·13	0·00	0·00	0·25	0·01	0·03	0·05	0·29
	1969–70	0·00	0·04	0·02	0·06	0·01	0·07	0·15	0·54
Nitrate-N	1968–69	20·4	12·2	20·4	8·2	3·2	7·9	10·8	2·0
	1969–70	24·5	12·2	21·4	11·7	5·0	10·9	9·0	1·9
Phosphorus	1968–69	0·08	0·02	0·43	0·09	0·07	0·22	0·15	0·01
	1969–70	0·02	0·00	0·33	0·03	0·05	0·22	0·05	0·01
Sulphate-S	1968–69	59	50	33	104	33	41	23	58
	1969–70	53	48	41	119	38	43	39	54
Chloride	1968–69	46	29	24	47	15	19	35	46
	1969–70	43	24	27	53	14	18	39	48
Conductivity (μ mhos/cm)	1968–69	880	770	470	1200	630	650	480	730
	1969–70	810	730	500	1230	610	530	550	680
pH	1968–69	7·1	7·3	6·3	7·4	7·2	7·1	7·1	7·5
	1969–70	7·2	7·4	6·6	7·8	7·5	7·2	7·3	7·5

most affected by leaching and, for this reason and because the amount leached depends on fertiliser–N applied, nitrate concentrations are discussed separately, with particular reference to the effects of rainfall intensity and evaporation on leaching.

Nitrate in drainage

Saxmundham. Figure 2 shows the relationships between monthly rainfall, rainfall greater than 10 mm daily, evaporation from open water surface (E_0) from May to September, and mean monthly flowrates (l/minute) from Drains 1–4, with corresponding mean monthly concentrations of nitrate in drainage for the three years 1967, 1968 and 1969. During 1967, rainfall during the first four months (158 mm) was less than in 1968 (178 mm) or in 1969 (213 mm). Evaporation (E_0) was greater in 1967 than in the two succeeding years and there was an accumulated moisture deficit (0·75 E_0 *minus* rainfall) of 166 mm by the end of September 1967. In 1968 the monthly deficit never exceeded 51 mm and by October there was a surplus of 89 mm of rain over evaporation from the heavy rainfall during August–September. In 1969 the accumulated moisture deficit was very small, rising only to 48 mm by the end of October, after two months of exceptionally dry weather. The relationships of rainfall and evaporation were reflected in the pattern of land drainage. When rainfall was small and evaporation large during May–September 1967, drainage stopped; by contrast, the drains ran throughout the summer of 1968. Exceptionally heavy rain in September 1968 induced very rapid flows containing large concentrations of nitrate. Very little rain fell during September 1969 and there was no

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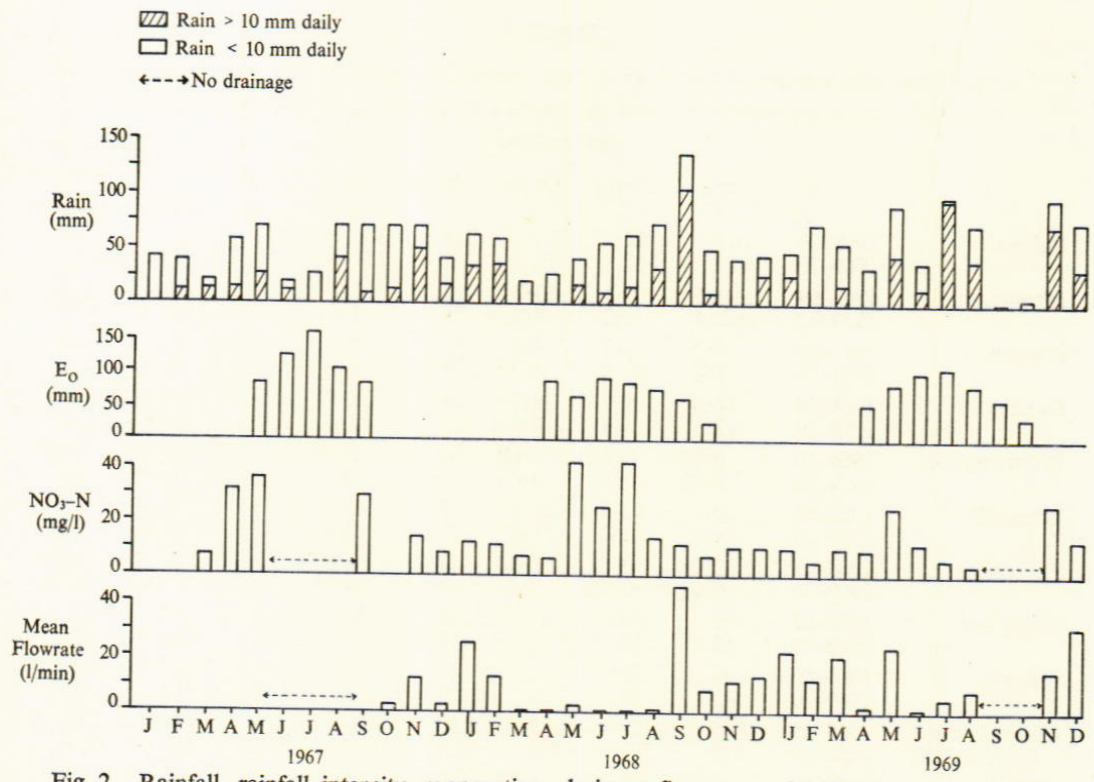

Fig. 2. Rainfall, rainfall intensity, evaporation, drainage flowrate, and NO_3-N concentration, in drainage at Saxmundham 1967–69.

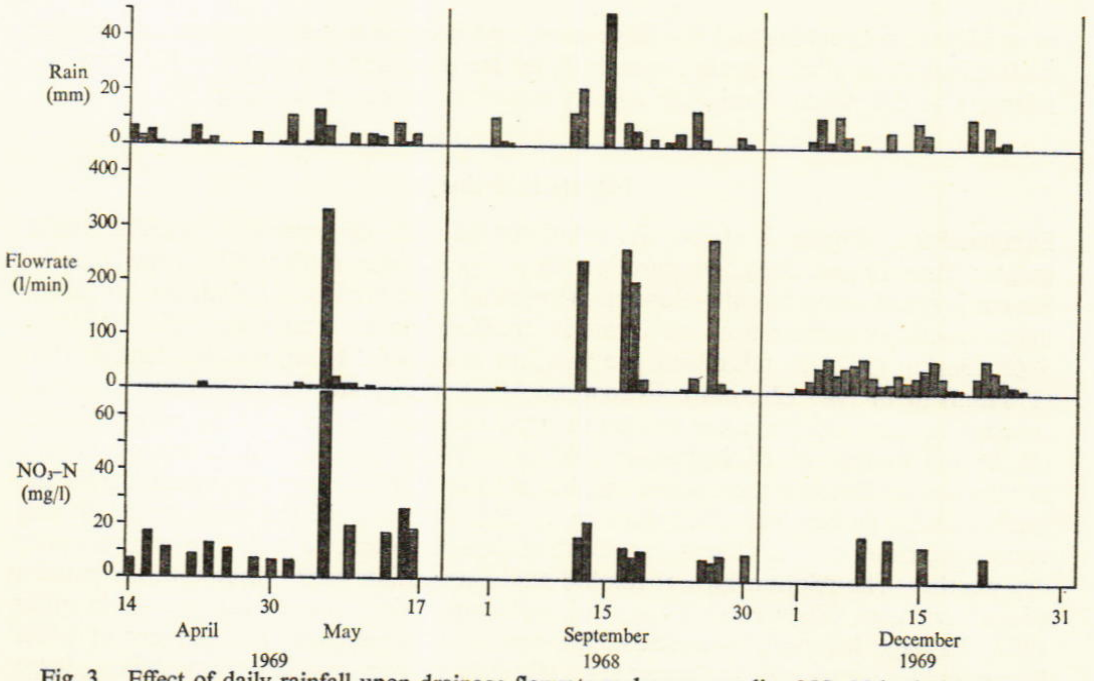

Fig. 3. Effect of daily rainfall upon drainage flowrate and corresponding NO_3-N in drainage water at Saxmundham.

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drainage during September and October. Spring rainfall determined whether freshly applied fertiliser nitrogen was leached. There were considerable falls in all three years and the drainage water contained much nitrate. There were large flows during the winter of 1967–68 and the water contained much nitrate. More was lost during May 1968 when moderate flows were rich in nitrate, indicating that leaching was still very active. Much nitrate was leached during the winter of 1968–69 when the drains flowed fast until March. Heavy, and at times intense, rain during March to August 1969 caused further large losses of nitrate, and fast flowrates were sometimes coupled with large concentrations of nitrate. Many crops grown in 1969 appeared deficient in nitrogen, and this was confirmed by tissue tests and responses to supplementary top-dressings of N-fertiliser.

Figure 3 shows that large amounts of rain falling in a day or less were associated with fast flowrates at Saxmundham. However, the amount of nitrate lost depended on weather patterns and times of applying N-fertiliser. In the first week of May 1969 there was a very large flow containing much nitrate, but before and after this, flowrates and concentrations of nitrate were much smaller. More than 10 mm of rain on each of two days before 6 May caused much drainage from the soil, which was already close to field capacity; these flows were responsible for the total loss (or transport into subsoil) of much freshly-applied N-fertiliser. In contrast, during December 1969, when the drains ran rapidly for most of the month, the flows caused by similar intensities of rain did not contain much nitrate. Freshly applied N-fertiliser, and nitrate derived from residues, are leached in different ways. September 1969 was very dry and there was no drainage. Figure 3 shows how the very wet September of 1968 caused large flows containing much nitrate, ranging from 7 to 20 mg/l NO_3–N, and although these flows in autumn removed much nitrate from the land, they differed in character from those in spring when the mean concentration in large flows was about 70 mg/l of NO_3–N.

Woburn. Most of the drains had large and relatively constant flows and nitrate concentrations did not show the large spring and autumn maxima found at Saxmundham. However, Drain 4 at Woburn, which serves an area of heavier textured soil, behaved similarly to Saxmundham drains. Figure 4 illustrates the differences during the two years between Drain 4 and Drain 1 at Woburn; Drain 1 originates in deep sandy soil in the higher part of Great Hill Field (Fig. 1). Drain 4 showed seasonal maxima in flowrates similar to the smaller peaks from Drain 1. The nitrate concentrations in water from Drain 1 did not vary greatly during the two years, but tended to increase when drainage was least. During the first two months of 1970, increased flow was accompanied by an increase in nitrate concentration in Drain 1. This could have been because residual nitrogen, accumulated during the dry September and October of 1969, was removed by the unusually large flows in February 1970; the smaller flow in March 1970 had a usual nitrate concentration.

Woburn, Saxmundham and Rothamsted compared. Figure 4 also compares Drain 2 on Harwood's Field and West Field Drain 6 for Saxmundham. During the two years, maximum flowrates from the West Field drain were much smaller. Comparatively small flows from Drain 2 had much nitrate during the spring and summer of 1968, and West Field drain did not run; both drains had maximum flows in May 1969. Although the concentration of nitrate in the West Field drainage exceeded that in the drainage from Harwood's Field, the flow from the West Field drain was only one-eighth as large. The nitrate concentrations in Drain 4 at Woburn and the West Field drain at Saxmundham were generally similar, but the Saxmundham drain had less nitrate during

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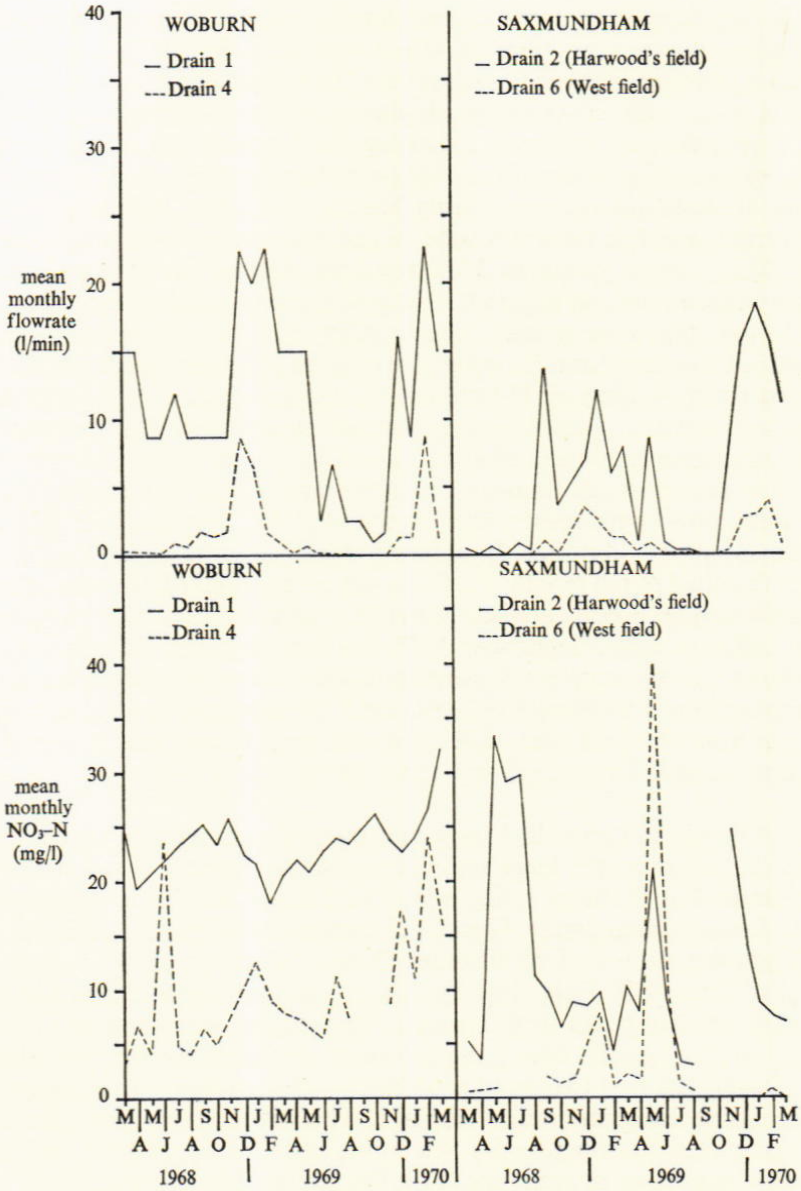

Fig. 4. Seasonal variation in drainage flowrates and corresponding NO_3-N concentrations at Woburn and Saxmundham 1968–70.

the first three months of 1969 and 1970. Tables 4 and 6 show that the mean annual concentrations of nitrate in Saxmundham drainage was 15·4 mg/l in 1968–69 and 12·2 mg/l in 1969–70; these are very similar to the corresponding figures for Woburn of 12·3 and 14·8 mg/l. However, at Saxmundham the daily concentrations ranged from $<$0·01 to 90 mg/l NO_3–N in very variable flows, whereas at Woburn, they were from 1·2 to 32·2 mg/l NO_3–N, with more constant flows. Table 5 shows concentrations of NO_3–N in water from the individual drains at Saxmundham. Drains 1 and 2 gave similar nitrate concentrations, which were less than those from Drains 3 and 4, and

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Drain 4 had smaller flowrates. On average, water from Drain 6 (West Field) had much smaller nitrate concentrations than water from the Harwood's Field drains, which also produced much larger flows.

These new measurements of nitrate concentrations in drainage confirm the work of a century ago on Broadbalk Field at Rothamsted, where a separate drain under each of the plots collects water; the experiment provided a unique opportunity of measuring losses of nitrate from plots fertilised with different amounts and kinds of N-fertilisers. The Broadbalk experiment is in 17 long parallel strips each of 0·2 ha; winter wheat has been grown each year since 1843. Tile drains 0·6 m deep were laid in the centre of each plot in 1849; they run for only a few hours after heavy rain and are dry most days of the year. Drainage water analyses begun in 1866 were continued for 15 years and were reported in several papers (Lawes & Gilbert, 1874; Lawes, Gilbert & Warington, 1882). Until 1872–73 ammonium salts were applied in autumn and nitrate in spring. Table 8

TABLE 8

Drainage from Broadbalk: average analyses for 1866–73 and seasonal changes measured in 1878–81

Plot	Annual manuring, kg N/ha	Average NO_3-N in drainage 1866–73 mg/l	1878–81; NO_3-N in drainage, mg/l				
			Spring fertilising to 31 May	1 June to harvest	Harvest to autumn sowing	Autumn to spring fertilising	Whole year
2	Farmyard manure (35 tons/ha)	12	4	1	6	10	8
3	None	4	3	0	5	5	4
5*	None	5	3	0	5	6	4
6*	48 as ammonium salts, in	9	15	1	6	5	5
7*	96 autumn until 1873; in	16	27	1	7	5	7
8*	144 spring 1878–81	20	28	4	14	8	9
9*	96 as nitrate in spring	16	50	9	15	8	12
15*	96 as ammonium in autumn	—	7	3	8	28	19

* These plots also receive annual dressings of PKNaMg fertilisers.

gives results for a later period (1878–81), when both ammonium salts (Plots 6, 7 and 8) and nitrate (Plot 9) were applied in spring. Much nitrate was lost from the 'natural' supply in farmyard manure, and water from this plot was richest in nitrate during autumn and winter. Drainage from land not given fertiliser (Plot 3), or not given nitrogen (Plot 5), contained 4–5 mg/l NO_3–N. From fertilised plots, spring drainage was richest in nitrate and there was a second peak early in autumn. During the second period (1878–81), when autumn and spring dressings were compared, the largest losses were from plots given ammonium salts in autumn (Plot 15); more nitrate was lost from nitrate fertiliser (Plot 9) than from equivalent ammonium salts (Plot 7) when both were applied in spring.

At both Saxmundham and Woburn, concentrations averaged 12–15 mg/l for the whole year, about the same as the amounts in Broadbalk drainage when 96 kg N/ha were applied as ammonium salts in autumn or all as nitrate in spring.

Other nutrients in drainage

Tables 4a and b show the monthly means, maximum and minimum concentrations of calcium, magnesium, potassium, sodium, ammonium-N, phosphate-P, sulphate-S and

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chloride, found in Saxmundham drainage water. Table 5 shows the mean annual concentrations of these ions, together with conductivity and pH of water from the individual drains. Tables 6a, b and 7 provide corresponding values for the Woburn drainage.

Calcium. The largest concentrations in the drainage water for both Woburn and Saxmundham were of calcium. Maximum and minimum concentrations in daily samples at Saxmundham were 280 mg/l and 62 mg/l, but monthly mean concentrations ranged much less. Exceptionally small values were associated with large rainfall. The mean annual values of 192 mg/l for the first year and 168 mg/l for the second year were larger than those for Woburn drainage (148 mg/l and 132 mg/l respectively). At Woburn, however, the concentration of calcium in Drain 4 from the Oxford Clay sometimes exceeded 360 mg/l, whereas Drain 3 had consistently less calcium (<86 mg/l). Larger variations in the composition of the water from different drains at Woburn than at Saxmundham show clearly how water composition depends on soil type. However, management of land can affect the relative concentrations of ions in drainage from the same kind of soil; less calcium was found in drainage water from Saxmundham West Field, which has poor drainage, than in Harwood's Field drainage during 1968–70. The stream at Woburn, which seems to be fed from an extensive and varied catchment, had less calcium than the land drains observed (except for No. 3), and its composition fluctuated less than the composition of land drainage during the two years, but flows greatly exceeded the flows from the land drains.

Magnesium

Saxmundham. The concentration of magnesium in Saxmundham drainage water ranged from 0·8 mg/l to 28·8 mg/l; more was present in 1968–69 than in 1969–70, which was wetter and drain flows were larger. Concentrations of magnesium diminished during winter, when flows were large, and increased during summer and autumn, except when there was much rain as during September 1968. Mean annual concentrations of magnesium were 9·5 mg/l for 1968–69 and 7·3 mg/l for 1969–70. The concentrations of magnesium in water from the separate drains at Saxmundham did not differ much, except that water from Drain 3, which had a smaller average flow than Nos. 1 and 2, contained slightly more Mg.

Woburn. Magnesium concentrations in the drainage ranged from 3·3 mg/l to 34·0 mg/l during the two-year period, but mean annual concentrations were almost the same. The least concentrations were in drainage during the very dry months of September and October 1969; these were followed in November and December by some of the largest values recorded. Large flows in February 1969, and in 1970, did not diminish magnesium concentrations much below the mean annual level. Concentrations in the individual drains differed. Water from Drain 4 from the Oxford Clay had most Mg, water from 5 and 6 had least, and that from Drains 1 and 3 had intermediate amounts. The large concentrations of magnesium in drainage at Woburn may derive from glauconite in the Lower Greensand, which is the parent material of the lighter soils at Woburn. Concentrations of magnesium in the stream resembled those in the drainage, except from Drain 4, which contained more.

Potassium

Saxmundham. Potassium in Saxmundham drainage ranged from 0·4 to 4·8 mg/l K. Usually there was less in the larger flows, although the largest concentration was in a

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flow of 60 l/minute from Drain 2 on 17 September 1968 (perhaps because there was dispersed clay in the water). Concentrations of K in the water from different drains were similar, which was expected as water comes from the same soil type; mean annual concentrations were 1·8 mg/l and 1·4 mg/l of K.

Woburn. By contrast, the concentration of potassium at Woburn differed between drains. Drain 4 from the Oxford Clay gave the most and Drains 2 and 5 the least. Drain No. 4 produced the largest individual concentrations in June of each year (up to 90 mg/l K), perhaps because its flow was always least and the water was longest in contact with soil. Mean annual concentrations of potassium in all the drains at Woburn (Table 6) were similar for both years, averages of 4·4 and 5·3 mg/l. Mean concentrations in the stream were 3·7 and 4·7 mg/l, with little change during the whole period.

Sodium

Saxmundham. The sodium in drainage during 1968–70 ranged from 7·4 mg/l to 44·8 mg/l Na; mean annual values were 21·6 mg/l for 1968–69 and 17·9 mg/l for 1969–70. Most was in water during March and April in both years, and mean monthly concentrations were least when rainfall, and drainage flows, were largest. After dry weather during autumn 1969 drainage ceased; the concentrations of sodium were not very large when drains ran again. Analyses of rain at Saxmundham (Williams, 1968) showed that sodium was the dominant cation and the amount in rain falling between December 1966 to November 1967 was equivalent to 8 kg/ha. Concentrations were larger during spring and autumn, especially when the wind was from the east, i.e. from the sea, which is 8 km away. Sodium can accumulate in soil when rain is not enough for drainage to occur.

Woburn. Woburn drainage contained only about half as much sodium as drainage at Saxmundham. Mean annual concentrations were 11·3 for 1968–69 and 11·1 mg/l for 1969–70. The maximum concentration found in the two years was 28·4 mg/l and the smallest 6·8 mg/l. Most was in water from Drain 4, which flows from the heavier land, possibly because flows from this drain were least. Pollution of drainage water by animals did not increase sodium, because Drain 6, which runs under land often grazed, gave rather less than the other drains from land that carries no stock. Sodium concentrations were not associated with rainfall or flowrates; the stream had almost the same mean annual concentration of sodium in both years, although total rainfall and its distribution differed greatly.

Ammonium-N. At both sites drainage water contained little NH_4–N, ranging from $<$0·05 mg/l to 3·0 mg/l NH_4–N at Saxmundham and from $<$0·05 to 3·2 mg/l NH_4–N at Woburn, but most measurements were less than 1 mg/l.

Mean annual concentrations at Saxmundham were 0·08 mg/l in 1968–69 and 0·16 mg/l in 1969–70, and at Woburn 0·07 mg/l and 0·03 mg/l; the largest value at Woburn was from Drain 4 serving the heavy soil. All four drains on Harwood's Field at Saxmundham and the West Field drain gave water containing more NH_4–N than usual in September 1968 when 108 mm of rain fell; this very wet period may have caused temporary waterlogging that inhibited nitrification and the rapid drainage removed ammonium-N (Fig. 3). Anhydrous ammonia was applied in March 1969 to an experiment on grass near Drain 3. Much rain next day caused large drainage flows of 40–60 l/minute and these contained unusually large amounts (1·4 mg/l) of ammonium-N,

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suggesting that freshly-applied ammonia can be leached from this soil soon after it is applied.

The stream at Woburn usually contained less than 0·05 mg/l of NH_4–N but had 0·5 mg/l from December to February, probably because there was little nitrification of soluble organic matter when soil temperatures were near freezing point.

Phosphorus. Concentrations of phosphate in the drainage water at Saxmundham and Woburn resembled those of ammonium-N and never exceeded 1·2 mg/l. At Saxmundham the range was <0·05 to 1·2 mg/l PO_4–P and mean annual concentration was 0·04 mg/l for 1968–69 and 0·06 mg/l for 1969–70; corresponding figures for Woburn were <0·05 to 0·85 mg/l PO_4–P, 0·15 and 0·12 mg/l PO_4–P.

At Saxmundham in 1968–69 the West Field drainage contained more phosphate than water from Harwood's Field but none was detected during the second year. At Woburn (Table 8), in contrast to other nutrients, Drain 4 did not give the most phosphate; mean annual concentrations of 0·09 mg/l and 0·03 mg/l for 1968–69 and 1969–70 were smaller than those from Drain 3 (0·43 and 0·33 mg/l) and Drain 6 (0·22 and 0·22 mg/l) respectively for the two years. We do not know the origin of the larger concentrations of phosphate (0·2 to 0·6 mg/l) in water from Drain 3, but the mains water at Woburn Farm, which comes from boreholes in the Greensand strata of the Birchmoor source, contains similar amounts. Water from Drain 3 but not from the others was slightly acid, and perhaps this makes native phosphate more soluble.

Water from Drain 6 probably contained some phosphate because the pipes are shallow and animal excreta may have penetrated to them. Drains 5 and 6 serve the same area but Drain 5 does not cross grazed land and always had less phosphate.

Much soluble phosphate in drainage was often associated with dispersed soil particles in the water. Drainage water at Saxmundham was turbid after autumn cultivations and after periods of severe frost followed by a thaw. Samples of water from Drains 2, 3 and 4 at Saxmundham on 26 September 1968 contained 255 to 490 mg/l of suspended solids and had 0·10 and 0·16 mg/l P. Twelve days later, there was less than 0·05 mg/l of P, although there were still 160 mg/l of suspended solids. During the same period, drainage from West Field had 622 mg/l of suspended solids; these diminished to 363 mg/l by 8 October, but soluble phosphate remained almost the same (0·36 mg/l). West Field is poorly drained and structure may degrade when the subsoil is anaerobic; reduction of ferric compounds may allow phosphate to dissolve, and these small (but larger than usual) amounts of soluble P to be leached.

Sulphur

Saxmundham. Sulphate in drainage water at Saxmundham averaged 62 mg/l in 1968–69 and 55 mg/l in 1969–70; during the two years the range was from 7 to 176 mg/l SO_4–S. Least sulphate was in water from Drain 4 after exceptionally heavy rain caused a large flow during mid-September 1968 (58 mm of rain fell during the previous three days). Most was lost in late April 1968 in water from Drain 3, after a period of dry weather, when the flow was very small (0·05 l/minute). Variations in sulphate in Saxmundham drainage water are discussed below in relation to changes in nitrate. Water from Drains 1, 2 and 3 of Harwood's Field contained larger concentrations of sulphate than water from No. 4 or from the West Field drain. Mean monthly sulphate concentrations were not closely related to mean monthly rainfall or to volume of drainage.

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Woburn. The mean annual concentrations of sulphate were 54 mg/l in 1968–69 and 56 mg/l in 1969–70, similar to those at Saxmundham. Concentrations also fluctuated similarly, from 15 to 163 mg/l SO_4–S, but there were contrasts between individual drains. Mean monthly concentrations in water from Drain 4 ranged from 85 to 156 mg/l of SO_4–S, and for the other drains from 15 to 103 mg/l, with the mean annual concentrations shown in Table 7. Monthly mean sulphate concentrations varied little during the two years although monthly rainfall and rainfall distribution varied greatly. The stream at Woburn contained less sulphate than the drainage water in both years, but concentrations were smaller and more varied during the first year when the flow was more constant. Least sulphate was recorded in September and October 1968 when there was much rain, and largest concentrations in December 1969 when flows increased again after the dry September and October.

Chloride

Saxmundham. Chloride in the drainage water averaged 48 mg/l in 1968–69, and 47 mg/l in 1969–70; the range for the two years was 16–129 mg/l Cl. Individual drains on Harwood's Field had similar concentrations, which were larger than those in West Field drainage.

Woburn. Chloride averaged 30·6 mg/l in 1968–69 and 36·6 mg/l in 1969–70, the range for the two years was 11·4 to 126 mg/l, very similar to the range at Saxmundham. The concentrations depended on the source, water from Drains 1 and 4 had most chloride and from Drains 5 and 6 least. The stream contained about as much chloride as water from Drain 1, giving a range of 29 to 46 mg/l during the two years.

Physical measurements on drainage water

Conductivity. The mean specific conductivity of the drainage water from Harwood's Field at Saxmundham was 949 μ mhos/cm in 1968–69 and 874 μ mhos/cm in 1969–70. The range during the two years was from 340 to 1420 μ mhos/cm. Water from individual drains differed; in the first year Drain 3, which gave the smallest and most intermittent flow, gave water with the largest conductivity, but in the second year conductivity was less, except for some large values in November 1969 after two dry months. Water from West Field had the smallest conductivities in both years; this drain flows slowly (resembling Nos 3 and 4 on Harwood's Field), but contains less soluble salts; this is unusual for drainage that flows slowly when the water is more nearly in equilibrium with soil constituents.

At Woburn, water from Drain 4 had largest conductivities in both years, 1200 μ mhos/cm in 1968–69 and 1230 μ mhos/cm in 1969–70. Water from Drains 3, 5 and 6 had least conductivity, ranging from 470 to 646 μ mhos/cm; Drains 5 and 6 gave similar results, especially during the first year. Drains 1 and 2 had intermediate values, ranging from 734 μ mhos/cm to 883 μ mhos/cm during the two years. The stream water had larger and slightly more variable conductivities in 1969–70 than in 1968–69, when flows were larger and more constant. Measurements of conductivity were very useful when considered with analyses for individual ions in the drainage waters; they were a check on composition, especially when there were large concentrations of individual ions while other ions remained relatively constant.

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Hydrogen ion concentration. The pH of drainage water at Saxmundham ranged only from 7·1 to 8·6, as the soil is calcareous. The values were close to the maximum associated with equilibrium calcium bicarbonate solutions. Differences between individual drains were very small.

At Woburn, water from Drain 3 had a smaller mean pH (6·3 and 6·6) in both years than from the other five drains or the stream, which averaged from pH 7·1 to 7·8 during the two years. Drain 3 varied from pH 5·8 to 6·9 in the first year and from 6·0 to 7·6 in the second year. The largest value recorded (8·2) was from Drain 4 in November 1969 after two dry months.

Relationships between the concentrations of nitrate and of the other ions in drainage water

Large drainage flows at Saxmundham during spring were always accompanied by sudden increases in nitrate concentration resulting from the rapid leaching of recently applied fertiliser. Changes in nitrate were associated with changes in the concentrations of ions other than the dominant calcium ion, which remained relatively constant at 250 mg/l. Figure 5 shows the relationships between SO_4^{--}, Cl^-, Na^+, and Mg^{++}, with increasing concentrations of NO_3^-.

Sulphate was more concentrated than other ions, except calcium; it was affected most by the changes that also caused nitrate to change, and diminished as nitrate increased. However, the sulphate concentration also showed a smaller, but significant, increase before the maximum concentration of nitrate was reached. When nitrate diminished after reaching a peak, sulphate concentration increased again to a near usual value. Because the drainage flow also diminished sharply with fall in nitrate concentration and sulphate had not increased enough to compensate, the conductivity of the drainage water was at a minimum. Sodium and magnesium concentrations, which were much less than those of sulphate, were affected similarly by the increase in nitrate, but the relative decreases were much smaller. Chloride behaved differently and showed a small peak coinciding with that of nitrate.

Potassium was much less concentrated than the other ions discussed; it fluctuated during the period when nitrate increased, but the fluctuations were not clearly related to changes in concentration of other ions, or to dilution and solubility effects. Saxmundham soil contains much readily exchangeable potassium and its solubility seemed to alter in the same way as that of calcium. Ca concentrations varied only from 212 to 280 mg/l during the period illustrated in Fig. 5 and the only large changes for this ion were after exceptional rain. On 16 September 1968, after 58 mm of rain during the previous three days, calcium fell to 115 mg/l and again to 86 mg/l on 26 September 1968 when a further 31 mm of rain had fallen. These small concentrations were presumably the result of the mass flow of rainwater, containing very little calcium, through leached and saturated soil; drainage was too fast for calcium salts in soil to reach equilibrium with the soil solution. In these conditions concentrations of sodium, magnesium, nitrate, chloride, and sulphate diminished and the corresponding conductivities were exceptionally small.

There were similar effects with Woburn drainage water, especially from the heavy land (Drain 4), but sampling was less frequent than at Saxmundham so the effects of rapid changes in nitrate concentration on the concentrations of other ions could not be examined.

The concentration of sulphate ions in drainage reached a peak that *preceded* the large

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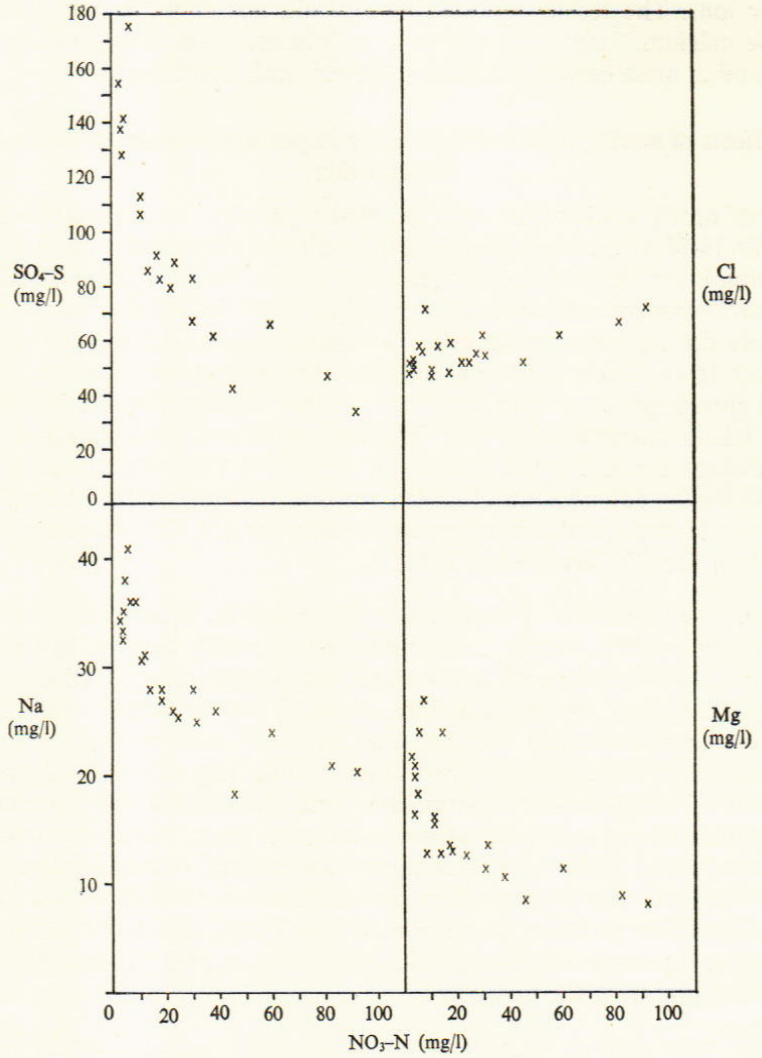

Fig. 5. Relationship between NO_3-N and SO_4-S, Cl, Na, and Mg in drainage at Saxmundham 3 April–10 May 1968.

peak in nitrate. This effect is similar to that in column chromatography when displaced molecules or ions occur in a band of greater concentrations detectable by collecting fractions of the solution. This band is followed by a peak concentration of the displacing species (in Saxmundham soil the very mobile nitrate ion in combination with the major soil cation (Ca)). Soil solutions cannot contain as much sulphate as nitrate, because the concentration of sulphate is governed by the solubility product of sparingly soluble calcium sulphate, which may not dissolve quickly enough to maintain normal concentrations of SO_4 during the rapid flows that leached the nitrate. Slower flows allow sulphate concentrations to become normal by solution from sites in the soil; but nitrate cannot be immediately renewed in the same way, so its concentration decreases rapidly. Cation/anion interactions in the solutions moving down soils in the field where modern fertilising is used should be studied more, especially the effects of much nitrate, and of calcium,

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on the other ions. The results reported here would not apply to acid soils with little exchangeable calcium. Important changes in drainage water composition occur very quickly; sampling must be very frequent to detect peak concentrations.

The effects of storing land drainage water in ponds and lakes on its chemical composition

Two bodies of nearly static water were sampled regularly. The farm pond 200 m south of Harwood's Field at Saxmundham is fed by ditches that receive land drainage. The catchment area is arable land, mostly growing cereals, which receive 70–120 kg N/ha/year; beans are also grown. No stock is kept and no animal effluent enters the pond, which overflows only during very wet periods. The artificial lake of about 0·4 ha at Woburn receives water from Drain 1 (it may have other underground sources we have not detected); it discharges only after very wet weather during summer, but often during winter. The lake is surrounded by our farmland, mostly in experiments in which large fertiliser dressings are used; the composition of its water was especially interesting because we knew the composition of its main source (Drain 1). Mean annual concentrations of ions, pH and conductivity measurements for the Saxmundham pond are in Table 5, and for the Woburn lake in Table 7.

Saxmundham. The analyses of pond water differed little between the two years. The concentrations of calcium, nitrate, and sulphur were smaller than in the drainage water from Harwood's Field; pH, conductivity and magnesium concentrations were similar but the pond contained more potassium, sodium, ammonium-N, phosphate-P and chloride. The nitrate from field drainage was no doubt removed by water plants. The water remained clear throughout the two years, without any bloom of algae. The larger concentrations of ammonium-N, potassium, and phosphorus were probably caused by decomposition of organic matter from weeds and trees, which surround the pond, and from water weeds. These ions were more concentrated during winter, when it was cold and water plants did not grow than during summer. Sulphate-S was least concentrated from September to December (down to 6 to 7 mg/l) and most during late winter and early spring (up to about 70 mg/l). Chloride was more constant, and ranged only from 50 to 70 mg/l during the two years.

Woburn. The mean annual concentrations of the ions measured in the Woburn lake water were also similar in the two years. The differences between land drainage composition and that of lake water were generally similar to those at Saxmundham; concentrations of sulphate and chloride were similar, but sulphate varied less than at Saxmundham. Calcium concentrations in Woburn lake were small during the dry September and October of 1969 and remained small until December. During the preceding (wetter) year calcium concentration fluctuated less. Monthly concentrations of ions in water from Drain 1 and the lake are interesting comparisons. Conductivity, calcium, phosphate, and especially nitrate, were smaller in the lake water. Magnesium, potassium, ammonium-N, and pH, were larger whereas sulphate and chloride were similar to the concentrations in water from Drain 1. Although 20 to 24 mg/l of NO_3–N entered the lake from this drain and there was enough soluble phosphate in the lake water to support algal growth (the minimum amount is thought to be 0·01 mg/l), no algal bloom occurred during the two years, the concentration of nitrate never exceeded 5 mg/l and was mostly less than 2 mg/l. The fate of the nitrate is not known but large water plants may remove it. The lake contains trout that thrive.

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Composition of water lying on the surface of land at Saxmundham

After heavy rain at Saxmundham, samples of water from shallow pools lying on Harwood's Field were analysed and their content of nutrients compared with that in drainage water sampled at the same time. The results show how nutrients can be lost in surface run-off from this land, which slopes to the south. Since 1964 the field has been ploughed deeply and accepts rainfall better, but before 1964 nutrients were probably carried in surface run-off to lower parts of the field or were lost altogether. Until recently the field was cultivated in the 'stetches' traditionally used in parts of East Anglia. Beds of land 3 m wide were shallowly ploughed and had surface drainage furrows between to remove the excess rain unable to penetrate into the cultivated layer.

Table 9 gives mean concentrations and ranges of ions in the surface water samples taken in 1968–69 and 1969–70. Only magnesium and sodium were less than the corresponding values for water from land drains. All the other ions (which were applied in fertiliser salts) varied considerably; nitrogen, phosphorus and potassium were very concentrated, especially during March to May of each year. The Saxmundham soil quickly 'caps' when there is much rain and plant nutrients, especially nitrate, whether added as fertiliser, or dissolved from the soil, could be easily lost by surface run-off down the field. Transport of this kind has occurred on the site of Rotation I Experiment, because crops on plots in the lower blocks have responded to nutrients washed over a central headland, and extra nutrients have been detected by soil analyses where fertilisers have not been applied. Small concentrations of nutrients in the drainage water from West Field may be partly because they are lost by the surface run-off, which has been observed.

Removal of crop nutrients in land drainage

The amounts of plant nutrients lost in land drainage depend not only on their concentrations and the corresponding flowrates of the land drains, but even more on how long the flows last. Large and protracted flows containing smaller concentrations may often be more significant in removing nutrients than spectacularly large concentrations in a short flow. Both composition and the flowrate of drainage water at Saxmundham differed from that at Woburn. At Saxmundham very large flows were often brief, but sometimes concentrations of ions were large. At Woburn continuous flows at moderate rates, and with moderate concentrations of ions, were recorded from deeper drains serving a much larger catchment.

The difficulties associated with estimating losses of nutrients in land drainage were well understood by Lawes and Gilbert when they investigated the composition of the drainage water from Broadbalk Field nearly 100 years ago. On Broadbalk the drains, laid 60 cm deep and overlying pervious subsoil over the chalk, receive only a small proportion of the total drainage as most of the water percolates between lines of tiles. To study the effect of flow on composition of the drainage, Lawes and Gilbert used a simple visual assessment of flows from the individual drains (Grey, 1922), similar to the one used here. Visual assessments were periodically checked by measuring the volume of drainage water collected during a known period. Mean monthly flowrates were calculated from daily records at Saxmundham, and from bi-weekly samplings at Woburn. These were used, together with the mean concentrations of the elements determined, to estimate nutrients lost in *observed* drainage. Lawes and Gilbert based their estimates of losses on *total* drainage occurring during the periods investigated, but the drainage was collected from an uncropped lysimeter 1·8 m × 2·2 m (0·0004 ha) and 1·5 m deep situated on

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TABLE 9

Composition of surface water at Saxmundham (Harwood's Field) 1968–70

Year		Na	K	Ca	Mg	NH_4–N	NO_3–N	PO_4–P	Cl	SO_4–S	K 25°C (μ mhos/cm)	pH
1968–69	Mean	11·8	8·3	108	3·9	3·0	7·2	1·24	62	35	689	7·7
	Range	6·2–21·2	1·0–33·5	30–242	1·5–8·7	0–30·2	0–39·7	0–9·70	14–175	11–112	200–1280	7·4–8·1
1969–70	Mean	7·0	3·8	77	2·2	0·5	13·2	0·18	22	22	430	7·7
	Range	3·8–10·8	1·2–11·2	37–107	1·3–4·2	0–2·1	0·9–47·6	0–1·67	4–73	9–41	200–710	7·0–8·6

TABLE 10

Total losses of nutrients from individual drains at Saxmundham (kg/year)

	Drain	Ca	Mg	K	Na	NH_4–N	NO_3–N	PO_4–P	SO_4–S	Cl
(1968–69)										
Harwood's Field	1	253	12	2·5	31	0·17	15	0·08	76	73
	2	318	16	2·0	37	0·10	21	0·03	112	73
	3	147	8	0·8	16	0·04	14	0·03	47	33
	4	46	2	0·6	5	0·01	5	0·02	10	16
	Total	764	38	5·9	89	0·32	55	0·16	245	195
West Field	6	48	3	0·8	6	0·03	1	0·05	14	13
(1969–70)										
Harwood's Field	1	369	14	4·6	42	0·37	25	0·17	109	125
	2	497	24	5·2	57	0·56	36	0·06	171	142
	3	139	6	1·2	15	0·15	11	0·01	55	35
	4	92	3	0·9	8	0·08	9	0·02	22	23
	Total	1097	47	11·9	122	1·16	81	0·26	357	325
West Field	6	57	4	1·0	6	0·10	3	0·00	22	14
Harwood's Field 1968–69 Total (kg/ha/year*)		252	12	1·9	29	0·1	18	0·05	81	64
1969–70 Total (kg/ha/year)		361	15	3·9	40	0·4	27	0·08	118	107

* Harwood's Field 3·03 hectares.

Barnfield and not on Broadbalk. This lysimeter was continuously fallowed, and they were aware that the drainage recorded was greater than from land that grew crops, although it might be similar for parts of the year when Broadbalk was bare or the crop very small.

At Saxmundham and at Woburn the drains are deeper than on Broadbalk; they overlie less pervious strata and must gather more of the total drainage. Flowrates at Saxmundham may have been over- or under-estimated, as they sometimes varied within one day; flowrates at Woburn were relatively constant and less frequent observations were satisfactory. More sophisticated measuring devices could have been used to measure the very small and very large flows, but it is questionable whether these would have been justified, because the proportion of *total* drainage collected by a tile drainage system is never known and it probably differs from season to season as subsoil drainage channels vary in capacity in dry and wet weather. In spite of these uncertainties, approximate estimates of nutrient losses seemed worth calculating to compare with those made for Broadbalk by Lawes and Gilbert. The figures are useful because they record the total amounts lost as surface drainage into ditches and streams. At Saxmundham *all* the other nutrients that are leached from Harwood's Field enter the deep subsoil and mobile ions may reach underground water reserves. The same is true at Woburn, but there may be other drainage channels to springs and streams that we have not detected. Tables 10 and 11 show estimated losses of nutrients. The losses at Saxmundham are also estimated as kilogrammes per hectare per year, because the drain outfalls on Harwood's are all known and they serve only this field; this could not be done for Woburn.

The greatest difference between nutrients lost in drainage at the two sites was that they were much greater for *individual* drains at Woburn. This resulted from the more constant, and on average larger, flowrates at Woburn. At Saxmundham the order of the amounts of individual ions lost was $Ca > SO_4\text{–}S > Cl > Na > NO_3\text{–}N > Mg > K > NH_4\text{–}N > PO_4\text{–}P$. At Woburn the order was similar except that more NO_3 was lost than Na, and more phosphate-P than ammonium-N. Saxmundham is close to the sea and receives extra sodium in rain, whereas Woburn is well inland. (The concentrations of sodium in the rain at Saxmundham and Woburn average 2·2 mg/l and 0·5 mg/l respectively). At Woburn the subsoils contain some phosphorus compounds that are more soluble and are leached more readily when the drainage water is acid (as with the Drain 3). The stream at Woburn removes considerable amounts of nutrients, with the proportions of individual ions in the same order as in drainage water at Saxmundham. The large amounts of calcium and nitrate removed each year by this small stream indicate the major losses there must be in larger rivers. The amount of nutrients removed by individual drains at Saxmundham reflect their different flowrates. Drain 2 carried most and Drain 4 least. The West Field drain removed much less as its flow is very small; the drainage was poor in nitrate and more magnesium and sodium than NO_3–N were lost in the two years.

Lawes and Gilbert (1882) constructed a balance sheet for Broadbalk showing relative losses and gains of nitrogen, but, as stated above, the absolute magnitude of their figures is uncertain because the amounts of drainage are unknown. However, these measurements are relevant to pervious soils overlying Chalk, which are common in Southern and Eastern England. Winter wheat is sown during autumn each year and Plot 7 receives about as much N-fertiliser as farmers apply (95 kg N/ha on average for England and Wales in 1969). For the year as a whole, drainage water passing into the Chalk will contain 7 mg/l of NO_3–N and, when there are 250 mm of drainage, 17 kg/ha of N from fertiliser will be lost. Where only organic manure is used (as in Plot 2), losses of nitrate might be larger. Even without fertiliser-N or organic manure (Plots 3 and 5), drainage

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TABLE 11

Total losses of nutrients from individual drains at Woburn (kg/year)

Drain	Ca	Mg	K	Na	NH_4–N	NO_3–N	PO_4–P	SO_4–S	Cl
				(1968–69)					
1	1176	67	13	101	0·91	144	0·56	414	327
2	807	36	4	52	0·00	65	0·11	263	155
3	121	18	8	15	0·00	35	0·74	57	42
4	230	17	16	16	0·25	8	0·09	104	47
5	370	20	10	29	0·09	23	0·63	118	56
6	246	10	1	16	0·02	6	0·13	63	29
1–6	2950	168	52	229	1·27	281	2·26	1019	656
Stream	5261	588	253	792	3·42	738	10·20	1558	2419
				(1969–70)					
Drain									
1	690	40	10	63	0·00	116	0·10	252	204
2	176	7	1	11	0·05	15	0·00	57	29
3	106	14	7	13	0·03	31	0·48	60	39
4	137	12	11	11	0·03	7	0·02	69	30
5	885	56	51	89	0·67	105	2·12	413	178
6	210	8	1	15	0·02	9	0·09	66	25
1–6	2204	137	81	202	0·80	283	2·81	917	505
Stream	3429	343	185	457	5·91	345	1·60	1553	1545

water would contain 4 mg/l of NO_3–N (average for the year), 11 kg N/ha would be lost (and yields would be less than a third of those with N-fertiliser or FYM). Losses of nitrate from spring-sown cereals given all their fertiliser-N between February and early April will probably exceed these on Broadbalk. (The average dressing for barley in England and Wales in 1969 was 80 kg N/ha.) Winter wheat transpires some water during spring, and drainage is less than from land under a spring-sown crop; the wheat also begins to take up nitrate by March and removes much in April, whereas spring-sown cereals take up little N until May. Losses of nitrate from Broadbalk Field from 1878 to 1881 were calculated by Lawes, Gilbert and Warington (1882). They estimated that 78 kg/ha N was lost during 1879–80 when 96 kg/ha N was applied as ammonium salts in autumn. When the same amount was applied as nitrate in spring, 68 kg/ha was lost in drainage. During 1880–81 the respective losses were 88 kg/ha and 63 kg/ha of nitrogen. The first winter was dry, the second very wet. The unfertilised soil lost 17 kg/ha N in 1879–80 and 21 kg/ha in 1880–81.

Raney (1960), who analysed leachates from lysimeters filled with Lakeland sand, concluded that the loss of cations was more closely related to the increase in nitrate than to the amount of water passing through the soil, when these were expressed as equivalent weights. Chloride and sulphate showed less association. Losses of nitrate in this work (Tables 10 and 11), were associated with the amount of total bases (Ca, Mg, Na, K) and with SO_4–S and Cl expressed as kilogramme equivalents a year. These relationships, shown in Fig. 6, were closer for Saxmundham than for Woburn drainage. Work on eight different soils from Illinois, used in the form of large, undisturbed, uncropped, and unfertilised cylinders was reported by Stauffer (1942). Surface run-off as a percentage of total rainfall on Muscatine silt loam was 22·4%, from Cowden loam it was 36·2%, drainage was 22·7% and 3·6% respectively. Loss of calcium was 95 kg/ha/year from the Muscatine soil and only 3·5 kg/ha/year from the Cowden loam. These results, although referring to lysimeter studies, illustrate the variations found in losses from different soil types, and emphasise the need for more information of this kind on field soils in the U.K.

For most British conditions, the total amounts of nutrients leached from farmland

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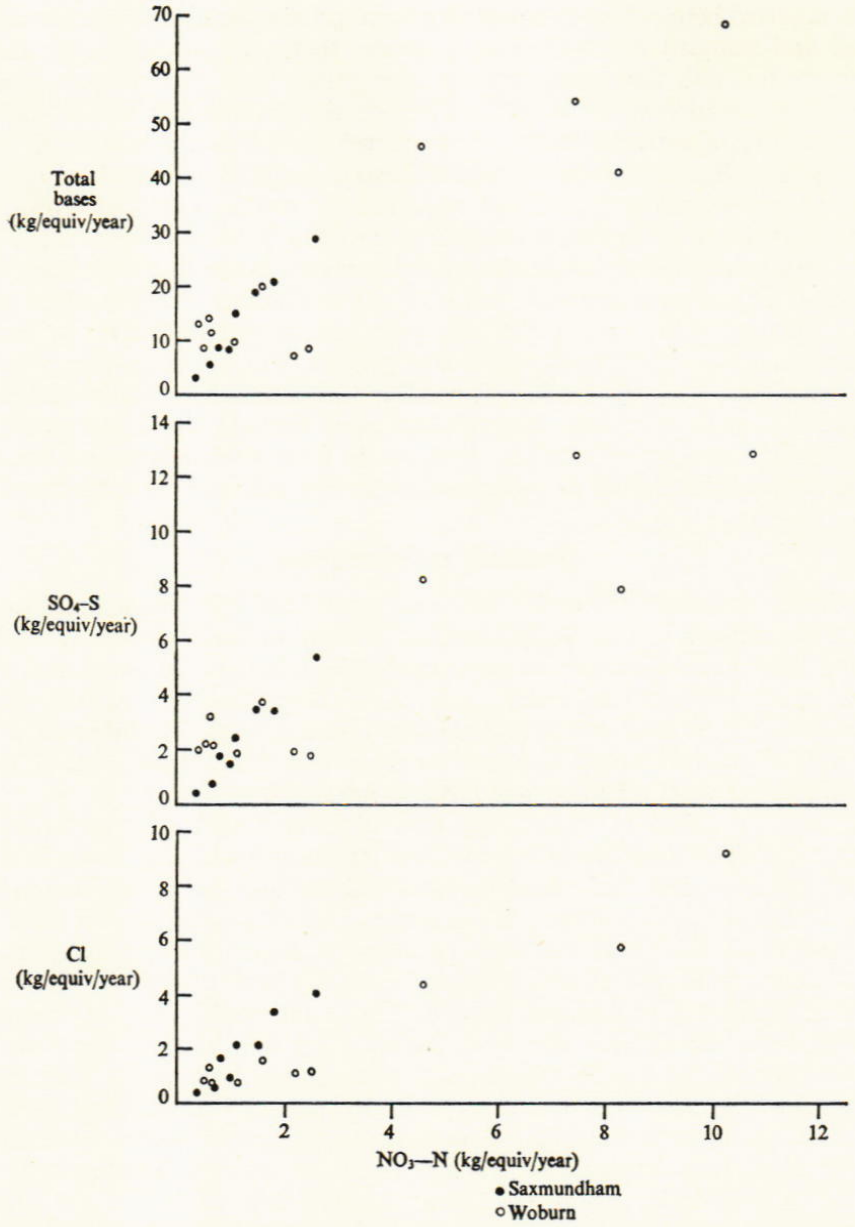

Fig. 6. Relationship between NO_3-N and total bases, SO_4-S, and Cl, in drainage at Woburn and Saxmundham 1968–70.

cannot be estimated accurately; percolating water, which displaces the soil solution, is never completely collected by any drainage system providing a flow that can be measured and sampled. The areas drained by ditches and streams can be assessed only rarely. On well-drained farmland, some of the water passes between the tiles into the deeper subsoil to reach a permanent water table. The proportion of water 'lost' in this way cannot be determined, but it must depend on the type of subsoil and parent material, and their physical condition (size and nature of cracks and fissures).

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Losses reported here can be regarded only as approximate, as they are based on flows measured and sampled intermittently. However, they serve to emphasise how much nutrients *are* lost and they show the need for greater care in fertiliser use and land management to avoid waste of fertilisers. The intensity of rainfall, which is the important factor in leaching of nutrients, cannot be predicted; but all that is practicable should be done to increase the proportion of rainfall that is accepted and retained by soils. Increasing the water-holding capacity of soils and the rooting depth of crops, by good management, helps to use both rain and soluble nutrients in soil solutions more efficiently. As more fertilisers are used, it becomes more important to use them efficiently. Nitrate–nitrogen and lime are the principal nutrients lost in drainage. Lime is cheap and costs British farmers only a few million pounds a year, but nitrogen fertilisers cost them about £70 million. If advisory officers assess drainage flows (which can be done visually) and measure the nitrate they contain (this is possible with a field test (Williams, 1969)), they can gauge the losses of nitrate. Assessments made through the winter could help in planning spring dressings of nitrogen; they would be even more valuable for assessing the losses from fertilised land in spring and indicating the need for extra top-dressings.

Summary and conclusions

Land drainage water from tile drains and from a pond and lake was sampled during two years at Saxmundham in East Suffolk, and at Woburn in Bedfordshire. A small stream at Woburn, and water from surface pools on fertilised land at Saxmundham, were also analysed, mainly by automated methods, for K, Ca, Mg, Na, NH_4–N, NO_3–N, PO_4–P, SO_4–S and Cl. Specific conductivity and pH were also measured. The influence of weather (mainly rainfall and its intensity) on the volume and the concentrations of all these ions was examined, but most attention was given to nitrate-N.

Drainage from a field of 3 ha of soil derived from boulder clay at Saxmundham, overlying a relatively impervious subsoil, was compared with the flows from deeper and more pervious soil derived from Lower Greensand overlying Oxford Clay at Woburn. Drainage flows from the boulder clay soil varied widely and depended on short periods with much rain (>10 mm/day). At Woburn, drainage flow was more constant and continuous, and depended on longer periods of dry or wet weather. A heavy Oxford Clay soil at Woburn gave drainage flows similar to the boulder clay at Saxmundham.

Drainage from the boulder clay and Oxford Clay soils showed sharp maxima in NO_3–N concentrations during spring; at Saxmundham these peaks were related to recently applied fertiliser–N. Much was lost in drainage at Saxmundham during spring when nitrate was more concentrated than during autumn and winter, when the nitrate came from residues of fertilisers or crops or from soil reserves. There was no marked nitrate maximum in drainage from the Greensand soils at Woburn. The mean concentration of nitrate 13·8 mg/l (at Saxmundham) and 15·5 mg/l (at Woburn) for the two years resemble those in drainage from Broadbalk Field at Rothamsted during the last century (12 mg/l) on the plot given 96 kg N/ha NO_3–N in spring. Sudden increases in nitrate concentration in drainage from the calcareous Saxmundham boulder clay soil caused corresponding decreases in SO_4–S, Cl, Na and Mg; Ca and K concentrations were not affected. Sulphate-S concentrations increased just before nitrate reached its maximum; chloride also increased (but less than sulphate) at the same time as nitrate.

The mean annual concentration of ions in the drainage water from Saxmundham (near the sea) were in the order

$$Ca > SO_4\text{–}S > Cl > Na > NO_3\text{–}N > Mg > K > NH_4\text{–}N > PO_4\text{–}P$$

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at Woburn (inland) NO_3–N > Na and PO_4–P > NH_4–N. The concentrations of ions in drainage diminished when flows were large, except when freshly applied nitrogen was being rapidly leached. Soil type influenced drainage composition at Woburn; ionic concentrations other than PO_4–P were greater in the Oxford Clay drainage than in Greensand drainage.

Soil management changed the composition of drainage water on the same soil type at Saxmundham, as the result of the imperfect working of recently laid tile drains. Phosphate-P and ammonium-N were usually less than 1 mg/l in drainage but phosphate was usually more than 0·01 mg/l recognised as being necessary for algal growth. Blooms of algae were not observed in the pond at Saxmundham or in the lake or stream water at Woburn.

The waters collected from a pond at Saxmundham and a lake at Woburn had different compositions from the drainage that fed them. Calcium, nitrate-N and sulphate-S were less; potassium, ammonium-N, phosphate-P and chloride were more in the pond and lake.

Surface water from shallow pools left after rain on boulder clay at Saxmundham contained less Mg and Na than drainage water, but more of other ions contained in fertilisers.

Estimates of the nutrients lost in *observed* drainage were calculated from mean annual flows and concentrations, but total losses cannot be determined as the proportion of drainage water that passes into subsoil between the tile drains is always unknown. The losses recorded emphasised that large amounts of nutrients were removed by drainage, especially lime and nitrogen, both of which farmers have to buy. Much more is spent on nitrogen than on lime, and using N efficiently becomes increasingly important as dressings increase. Also, lessening the nitrate that enters water used for public supply will help water authorities. Drainage flows can be estimated visually and their nitrate concentrations can be measured in the field; doing so might be a valuable aid in planning nitrogen fertilising.

APPENDIX

Methods of analysis and sampling used for the drainage water

Sampling and flowrate measurement. All samples of drainage water were collected in clean polythene bottles, stored in a cool place in the dark, and delivered as soon as possible to Rothamsted for analysis. Ammonium- and nitrate-nitrogen were measured immediately and the samples were stored in a refrigerator until other analyses were completed.

Flows from tile drains were first calibrated by measuring the volume in a known time. Subsequently, visual estimates of flow were found to agree closely with these volume/time measurements; these assessments were used later with periodical checks. It is immaterial how the visual estimates are made, so long as a constant scale is used that is not so fine that there is a risk of confusion between adjacent values. Rates slower than 30 l/minute are easy to estimate visually; larger flows, which transport much nutrients, even during a day and with concentrations of >25 mg/l, should be verified by measurement. Grey (1922) described the empirical equivalents used by Lawes, Gilbert and Warington (1882) for visually assessing the flows from the Broadbalk drains to investigate the effect of flow on drainage composition.

Potassium and sodium. By 'EEL' flame photometer.

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Calcium and magnesium. By a 'Unicam' SP 900 flame spectrophotometer with radiation buffers (Salt, 1967). Magnesium by atomic adsorption.

Ammonium-N. Absorptiometrically, using a 'Technicon AutoAnalyzer' and the method of Varley (1966) modified by adding a citrate/tartrate buffer; forty samples an hour were done and the limit of detection was 0·05 mg NH_4–N/l.

Nitrate-N. Absorptiometrically, using a 'Technicon AutoAnalyzer' and Litchfield's (1967) method. Twenty samples an hour were done with a limit of detection of 0·01 mg NO_3–N/l.

Phosphorus. Absorptiometrically, using a 'Technicon AutoAnalyzer', by Fogg and Wilkinson's (1958) method. Sixty samples an hour were measured with a limit of detection of 0·05 mg PO_4–P/l.

Chloride. Absorptiometrically, using a 'Technicon AutoAnalyzer' and Henriksen's (1966) method. Forty samples an hour were measured with a limit of detection of 0·5 mg Cl/l.

Sulphate. Turbimetrically, using a 'Technicon AutoAnalyzer' by the method of Williams and Twine (1967). Twenty samples an hour were measured with a limit of detection of 0·1 mg SO_4–S/l.

Conductivity. Using a 'Mullard' conductivity meter.

pH. Using a 'Pye' pH meter and a glass electrode.

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Results of the Rotation I Experiment at Saxmundham, 1964–69

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Rotation I experiment was started by the East Suffolk County Council in 1899. The four course practised until 1969 was: 1, Wheat; 2, Roots; swedes or turnips in the early years, then usually mangolds until 1964; from 1956 to 1964 mangolds and sugar beet were grown side by side on half-plots: 3, Barley: 4, Legume; usually beans but sometimes clover, peas often between 1940 and 1964. From 1965 to 1969 only beet and beans were grown on the root and legume breaks. Each crop was grown on one block of the experiment each year.

Classical treatments. The manurial treatments, unchanged from 1899–1965 and listed in Table 1, were applied annually to the same plots in each of the four blocks. The treatments had the full factorial arrangement of N, P and K, but were not randomised, and repeated in each block in the order listed in Table 1. Until recently, the manures used were not analysed and the nutrients applied are estimates based on probable average compositions. The figures for FYM are based on analyses of samples used at Saxmundham from 1964 to 1969; average contents were:

22% dry matter, and
3·3% N, 1·2% P and 2·1% K in dry matter.

Sodium nitrate probably had nearly constant %N but %P in superphosphate and %K in muriate of potash must have increased, especially since 1940. Two cwt/acre of superphosphate were applied each year; assuming that this was usual commercial material it will have contained 12–14% P_2O_5 at the beginning of the period and 20% P_2O_5 at the end; the figures in Table 1 assume an average of 16% P_2O_5. Similarly, the muriate of potash also changed, probably from 50% K_2O (or less) from 1900 to 1950 to 60% K_2O by 1960; the K supplied in Table 1 assumes an average analysis of 50% K_2O.

The experiment was described by Oldershaw (1941) and Trist and Boyd (1966), who summarised the yield results from 1899 to 1962. Crops were never systematically sampled and analysed until 1965. Cooke, Mattingly and Williams (1958) calculated a rough balance sheet for the period 1901 to 1956, using average compositions of crops from other experiments, and compared the results with analyses of soils taken from each plot in 1957.

New manuring treatments. In autumn 1965 most of the treatments were modified. The 'new' manuring (described on p. 74) was applied to six-sevenths of each plot, but a square sub-plot with 6 yd sides in the lower section of each block continued to receive the 'classical' manuring listed in Table 1, except that 12 tons/acre FYM was applied to Treatment 1. The sub-plots provided continuity with past results and the crops grown from 1964 to 1969 were analysed to make a balance sheet relevant to the main period of the experiment. They also provide soil for laboratory and pot experiments. In 1970 the cropping was greatly changed, for lucerne was sown on one one-half of each plot and grass on the other; manuring was little altered.

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TABLE 1

Experimental treatments in Rotation I experiment at Saxmundham in the classical period

Treatment number	Symbol	Treatment per acre	Plant nutrients applied annually (approximate estimates) N	P (lb/acre)	K
1	FYM	6 tons farmyard manure	98	35	61
2	BM	4 cwt bone meal	16	43	—
3	N	2 cwt nitrate of soda	35	—	—
4	P	2 cwt superphosphate	—	16	—
5	K	1 cwt muriate of potash	—	—	47
6	O	No manure	—	—	—
7	PK	2 cwt superphosphate + 1 cwt muriate of potash	—	16	47
8	NK	2 cwt nitrate of soda + 1 cwt muriate of potash	35	—	47
9	NP	2 cwt nitrate of soda + 2 cwt superphosphate	35	16	—
10	NPK	2 cwt nitrate of soda + 2 cwt superphosphate + 1 cwt muriate of potash	35	16	47

Cultivations. Two changes in management were made that affect results: 1. The whole field was mole-drained in 1964 and afterwards was ploughed, all one way, with a reversible single-furrow deep plough. The old ploughing depth was 5–6 inches (or shallower where the subsoil was compact). The new plough worked 10–12 inches deep and roughly doubled the depth of cultivated soil. 2. From 1965 cereals have been combine-harvested (the plots have no 'blank' rows) and from 1967 beans also. Yields of straw from the main plots after 1965 are not comparable with earlier yields when crops were cut by binder and threshed. On the small plots which continue the classical treatments, cereals have been harvested by hand and straw yields are comparable with the past.

This paper reports results from the experiment from 1965 to 1969, both for the 'classical' and the 'new' treatments. Yields and crop compositions were used to calculate the nutrients removed; analyses of soil from the main plots and the sub-plots in 1969 were compared with analyses in 1957 and 1966 to show how changed manuring and deeper ploughing since 1965 had altered nutrient reserves.

Varieties. Cappelle Desprez wheat has been grown each year since 1964; sugar beet has been Klein E. Proctor barley was grown from 1964 to 1967, Zephyr was used in 1968 and Sultan in 1969. Spring tick beans were grown in 1966 and 1967, Maris Bead in 1968 and 1969.

Results from the classical treatments, 1964 to 1969

Yields. Average yields from the classical treatments for the whole period of the experiment, given by Trist and Boyd (1966), are compared in Table 2 with yields since 1964.

In 1964–69 unmanured wheat and beans yielded a little more, and barley a little less, than average yields for the first 60 years of the experiment. Yields of unmanured beans were almost identical in 1905–18 (Trist & Boyd, 1966) and in 1967–69. There was no

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Table 2

Yields per acre of crops grown in Rotation I experiment at Saxmundham with Classical treatments

Wheat (cwt of grain)

Treatment number	Treatment	1900–61	1964	1965	1966	1967	1968	1969	Average 1964–69
6	None	10·2	13·9	18·2	—	9·1	19·8	3·9	13·0
3	N	13·9	21·3	24·6	—	19·5	31·9	9·9	21·4
4	P	13·8	19·7	15·9	—	15·8	23·7	8·7	16·8
5	K	10·1	9·9	13·9	—	12·9	18·1	5·9	12·1
9	NP	19·0	27·4	24·3	—	29·1	34·2	11·9	25·4
8	NK	15·0	20·8	26·5	—	22·2	27·5	7·4	20·9
7	PK	14·6	18·1	16·9	—	15·3	19·5	6·5	15·3
10	NPK	19·4	25·2	24·8	—	32·4	36·0	16·7	27·0
1	FYM	18·9	25·3	29·4	—	35·1	36·9	10·6	27·5
2	Bone meal	14·3	18·2	20·9	—	15·9	28·8	9·8	18·7

Barley (cwt of grain)

6	None	8·2	2·8	6·4	—	6·3	11·2	6·6	6·7
3	N	10·9	11·7	12·4	—	12·7	18·8	8·5	12·8
4	P	10·0	5·2	5·4	—	11·7	10·9	8·7	8·4
5	K	8·0	2·0	3·7	—	7·7	9·1	6·2	5·7
9	NP	17·0	14·4	23·6	—	15·8	25·9	13·4	18·6
8	NK	12·2	11·1	8·8	—	12·6	18·9	8·8	12·0
7	PK	11·1	3·1	5·9	—	8·1	13·4	9·1	7·9
10	NPK	18·0	16·1	21·2	—	17·5	23·5	10·8	17·8
1	FYM	16·2	21·3	23·2	—	16·6	28·9	19·0	21·8
2	Bone meal	10·7	7·4	9·8	—	14·2	10·9	9·7	10·4

Beans (cwt of grain)

		1905–61*	1967	1968	1969	Average 1967–69
6	None	10·9	8·0	15·5	16·4	13·3
3	N	11·3	11·5	23·1	12·5	15·7
4	P	17·0	16·4	24·3	15·2	18·6
5	K	11·4	8·2	13·7	10·1	10·7
9	NP	16·9	19·2	23·7	13·7	18·9
8	NK	12·1	12·0	24·8	19·5	18·8
7	PK	20·1	15·6	29·2	16·1	20·3
10	NPK	20·8	19·3	30·4	14·3	21·3
1	FYM	21·7	17·2	31·3	18·9	22·5
2	Bone meal	15·3	21·0	24·6	7·0	17·5

* 33 crops of beans and 18 of peas.

Sugar beet (tons of fresh roots)

		Average 1956–65	1964	1965	1966	1967	1968	1969	Average 1964–69
6	None	2·3	1·1	1·4	3·5	4·7	5·1	0·6	2·7
3	N	3·0	0·7	2·9	4·4	9·1	5·7	1·5	4·0
4	P	6·2	3·1	7·6	5·0	5·8	7·2	5·4	5·7
5	K	2·8	0·6	2·4	2·1	4·2	6·4	0·8	2·7
9	NP	9·6	5·5	10·2	12·7	9·4	11·9	6·4	9·3
8	NK	2·4	0·9	0·9	3·7	9·6	4·7	0·4	3·4
7	PK	6·0	2·3	6·8	7·3	7·0	8·4	4·5	6·0
10	NPK	10·0	7·1	11·0	11·2	8·5	12·7	4·6	9·2
1	FYM	13·1	9·8	13·9	11·1	12·4	18·5	11·8	12·9
2	Bone meal	7·2	3·2	10·0	5·4	5·8	8·6	5·6	6·4

Notes—1. In 1966 the wheat plots were not established and the barley was so poor it was not harvested.
2. The peas sown in 1964 and the beans in 1966 failed. The legume break was fallowed in 1965.
3. In this and later Tables cereal yields are given as cwt of grain containing 15% of moisture.

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suggestion that the small productivity of the soil was further diminished by growing crops for nearly 70 years without manure. Direct comparisons of yields of manured wheat and barley over the whole period cannot be made because different varieties with greater potential yield were grown after 1960. All wheat given N and P fertiliser in 1964–69 yielded more than the long-term averages. Modern barleys yielded no more with most treatments in 1964–69 than the older varieties grown between 1900 and 1919; FYM gave consistently larger yields during the last period (but the dressing was doubled for the last four crops). Mangolds were not grown after 1964; yields of beet in 1964–69 were very similar to those in the previous ten years. Average yields of the three bean crops grown were similar to those obtained between 1905 and 1918.

Trist and Boyd (1966) discussed changes in crop yields and main effects of fertilisers for three sets of 20-year averages between 1900 and 1961. Table 3 gives corresponding results for 1964–69. (The table also contains 'main effects' of the new treatments; these are discussed later.)

TABLE 3

Main effects of fertilisers and their interactions in Rotation I experiment

	Wheat (cwt/acre)					Barley (cwt/acre)				
	1900–19	1920–39	1940–61	1964–69	1966–69	1900–19	1920–39	1940–61	1964–69	1966–69
No. of years	20	20	22	5	4	20	20	22	5	4
	Classical treatments				New treatments†	Classical treatments				New treatments†
N	2·6	4·7	6·6	9·4	(6·4)	4·4	4·8	6·3	8·1	(6·1)
P	2·6	5·1	5·4	4·2	(−0·6)	2·4	3·9	5·8	3·9	(−1·6)
K	0·2	0·8	0·7	0·3	1·7	0·6	0·8	0·7	−0·7	−1·2
NP	0·2	0·3	0·6	0·8	—	1·0	1·6	2·1	1·9	—
NK	0·0	0·4	0·2	0·9	—	0·1	0·4	0·4	0·0	—
PK	−0·2	0·2	0·2	0·4	—	0·4	−0·2	0·4	0·1	—
NPK	−0·2	−0·4	−0·6	0·7	—	−0·2	−0·4	−0·6	−0·1	—

	Beans (cwt/acre)					Mangolds and sugar beet (tons/acre of roots)				
	1905–18	1920–39	1940–61*	1967–69	1966–69	1900–19	1920–39	1940–61	1964–69	1966–69
No. of years	14	15	16	3	9	14	20	22	6	4
	Classical treatments				New treatments	Classical treatments				New treatments
						Mangolds			Sugar beet	
N	0·4	0·1	0·8	2·9	1·3	3·0	3·2	4·2	2·2	(2·9)
P	7·4	8·3	6·1	5·2	(−1·4)	7·2	11·3	11·0	4·3	(−0·5)
K	1·4	2·8	2·1	1·1	3·0	0·2	0·6	1·0	−0·1	−0·4
NP	−0·2	−0·3	0·0	−2·3	0·6	2·0	2·6	2·4	1·2	—
NK	0·3	0·3	0·3	1·6	1·1	0·0	0·2	0·4	0·3	—
PK	1·2	1·7	1·3	0·9	−1·5	0·2	0·1	0·4	0·2	—
NPK	0·1	0·4	−0·1	−1·2	1·2	0·0	−0·2	−0·1	0·0	—

* Beans and peas.

† Main effects of new N and P treatments are in parentheses because they are *differences* between rates of fertilisers, not main effects as normally presented.

Cereals. Responses to nitrogen by wheat and barley have increased steadily through the whole 70 years. Responses to phosphorus have been less since 1964 than in the previous 20 years. Both crops gave small responses to potassium from 1900 to 1961, but

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the response by wheat in 1964–69 was less than previously and that for barley became negative. The only substantial interaction was for NP.

Beans gave small responses to N throughout the period and larger responses to K; phosphate had the largest effects, as for other crops. There was a consistent positive PK interaction with beans, response to K increasing with P, but it was not larger at the end than at the beginning of the experiment.

Sugar beet yielded smaller weights of roots than mangolds, but responses to N and P were proportionally similar. Mangolds gave small responses to K, which slightly depressed sugar-beet yields. The only large and consistent interaction with beet was of N with P.

There were two important trends: 1. Nitrogen responses tended to increase throughout the period. 2. Potassium responses did not increase. (Trist and Boyd (1966) also commented on the increases in nitrogen responses and suggested that %N in the soil had diminished during the experiment.) The capacity of the soil to supply K has continued undiminished for the 70 years. The small responses to K by wheat, barley and beans, shown from the start of the experiment, diminished for wheat and beans, and became negative for barley in 1964–69. The land has been ploughed twice as deeply since 1965 and the capacity of the soil to supply K may have been increased by cultivating layers that were previously subsoil.

Nutrient balance. Table 4 shows average amounts of nutrients removed by the crops grown between 1964 and 1969. A balance sheet relevant to the 'classical' period calculated from additions (Table 1) and losses in crops (Table 4) is in Table 5.

Until about 1950, FYM for the experiment was made by fattening bullocks housed in winter on the Station, and Oldershaw (1941) suggested it was 'of average quality'. The samples used since 1964 have come from a nearby dairy farm; their analyses were:

	Dry matter %	Per cent in dry matter					
		N	P	K	Ca	Mg	Na
Average	22·1	3·31	1·17	2·07	2·75	0·73	0·36
Range	19·3–28·8	2·45–3·91	0·74–1·75	1·32–2·46	1·88–3·48	0·27–1·63	0·20–0·62

Such manures provided more total nitrogen in a 6 tons/acre dressing than crops removed. The P supplied by 6 tons/acre must have been *much* more than crops removed annually since 1900, but on the basis of these analyses the K supplied has been less than crops grown with FYM contained.

Because losses of N by leaching and denitrification cannot be estimated, and the amounts fixed by legumes and by non-symbiotic organisms are not known, a true balance sheet for nitrogen cannot be calculated. However, Table 5 shows that fertilisers never supplied as much N as crops removed, even where growth was limited by phosphate deficiency. With P, but without N, the four crops have obtained about 200 lb/acre. Table 4 shows that beans fixed, on average, more than 100 lb N/acre/year and wheat has benefited from the residues left by the legumes. Barley receiving only PK fertiliser obtained about 14 lb N/acre from soil or other natural sources, sugar beet about twice as much.

Phosphorus supplied has always been more than crops removed from treated plots. The K supplied exceeded that removed where yields were restricted because neither N nor

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TABLE 4

Amounts of nutrients (in lb/acre) removed each year by crops grown with 'classical' treatments in Rotation I experiment at Saxmundham, 1964–69

	FYM	BM	N	P	K	O	PK	NK	NP	NPK	Mean
Nitrogen											
Wheat	64·9	36·1	42·5	32·4	24·1	25·4	30·7	43·2	50·0	55·3	40·4
Barley	38·4	18·7	22·7	14·2	11·7	12·0	13·7	23·1	29·8	30·2	21·5
Beans	122·3	103·7	82·4	108·1	56·6	73·5	114·3	100·9	112·5	120·7	99·4
Sugar beet	76·2	36·9	28·8	29·8	17·9	22·0	30·7	31·2	49·4	49·8	37·3
Total of four crops	301·8	195·4	176·4	184·5	110·3	132·9	189·4	198·4	241·7	256·0	198·6
Phosphorus											
Wheat	14·0	7·6	6·8	7·3	4·3	4·5	7·0	6·8	10·3	11·3	8·0
Barley	10·0	4·1	4·2	3·4	2·0	2·3	3·3	4·0	7·4	7·5	4·8
Beans	14·3	9·9	5·6	10·8	3·4	4·3	11·2	5·9	12·3	13·1	9·1
Sugar beet	16·5	7·9	3·5	7·0	2·6	3·5	7·2	3·0	11·6	11·3	7·4
Total of four crops	54·8	29·5	20·1	28·5	12·3	14·6	28·7	19·7	41·6	43·2	29·3
Potassium											
Wheat	49·2	22·9	25·2	20·4	17·0	17·4	21·4	27·8	31·0	37·7	25·0
Barley	30·6	12·4	15·2	9·7	8·0	8·0	10·0	18·9	18·6	21·7	15·3
Beans	81·4	25·6	20·2	23·5	25·4	20·2	42·0	42·2	25·9	44·2	35·0
Sugar beet	164·4	70·9	47·7	65·4	42·3	43·5	70·7	47·8	93·0	107·3	75·3
Total of four crops	325·6	131·8	108·3	119·0	92·7	89·1	144·1	136·7	168·5	210·9	150·6
Calcium											
Wheat	13·1	7·9	8·0	7·0	4·6	4·3	6·0	6·9	9·7	10·9	7·8
Barley	9·0	4·5	5·5	3·9	2·6	3·1	4·2	5·6	7·8	8·1	5·4
Beans	26·5	24·8	16·3	21·8	12·5	14·3	28·2	20·6	24·0	29·1	21·8
Sugar beet	41·8	23·3	20·1	22·9	13·9	15·1	22·0	18·5	33·7	34·3	24·6
Total of four crops	90·4	60·5	49·9	55·6	33·6	36·8	60·4	51·6	75·2	82·4	59·6
Magnesium											
Wheat	6·4	3·5	3·5	3·3	1·9	2·1	2·8	3·5	4·7	5·3	3·7
Barley	4·3	1·9	2·2	1·5	1·0	1·1	1·4	2·1	3·5	3·5	2·2
Beans	5·4	4·3	3·6	4·4	2·4	2·9	4·5	3·8	4·7	4·7	4·1
Sugar beet	20·9	10·1	7·0	8·7	4·7	5·5	8·3	5·9	13·8	12·9	9·8
Total of four crops	37·0	19·8	16·3	17·9	10·0	11·6	17·0	15·3	26·7	26·4	19·8
Sodium											
Wheat	0·9	0·6	0·7	0·5	0·4	0·4	0·5	0·7	0·8	0·9	0·6
Barley	1·3	0·6	1·4	0·5	0·3	0·4	0·4	1·1	1·9	1·4	0·9
Beans	6·2	21·0	17·7	18·6	2·9	9·1	12·9	8·1	24·4	16·7	13·7
Sugar beet	26·7	13·2	17·0	9·2	4·5	7·1	7·0	10·5	21·9	19·2	13·6
Total of four crops	35·1	35·4	36·8	28·8	8·1	17·0	20·8	20·4	49·0	38·2	28·8

TABLE 5

Estimates of annual changes caused by classical treatments in nutrients in the soils of Rotation I experiment for 1964–69

Treatment number	Treatment	lb/acre N	P	K
6	None	−33·2	−4	−22
3	N	−9	−5	−27
4	P	−46	+9	−30
5	K	−28	−3	+23
9	NP	−25	+6	−42
8	NK	−15	−5	+13
7	PK	−47	+9	+11
10	NPK	−29	+5	−6
2	Bone meal	−31	+33	−32
1	FYM (at 6 tons/acre)	+23	+21	−20

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P was given. NPK fertilisers applied to Treatment 10 supplied a few pounds less K than crops removed.

Without P fertiliser, the crops with N and K removed about 5 lb P/acre/year from the soil, wheat most and sugar beet least. Crops without K fertiliser (but with N and P), removed about 40 lb K/acre/year from the soils, sugar beet several times as much as cereal or beans.

The average annual balance for N, P and K shown in Table 5 is relevant to the period of classical manuring since 1900; average crop yields in 1964–69 were near to the long-period averages and there is no reason to expect crop compositions to have varied greatly. The figures suggest that, in 70 years, crops have removed about 350 lb P/acre where they received N and K fertilisers but no phosphate (roughly equivalent to 175 ppm P in the top soil). About 2800 lb K/acre has been removed by crops receiving N and P but not K, which is equivalent to 0·14% K in the top-soil (assuming that the old ploughed layer, which was about 5 inches deep, weighed 2 million lb/acre).

Results from the modified experiment, 1965–69

New treatments. In 1965 we saw no point in continuing the demonstration on whole plots that unfertilised crops at Saxmundham yield little, that phosphate fertiliser is essential, and that much nitrogen is needed for all crops but legumes. The treatments given to the main part of nine of the ten plots in each block were modified for the crops harvested in 1966. (Sub-plots 6 yds long, out of the total length of 44 yds, retained the classical treatments). Only the bone meal dressings (Treatment 2) remained unchanged. The FYM dressing was doubled to 12 tons/acre and, in all years except 1966, 56 lb N/acre was applied to the main plots. The fertiliser tests are described below. The existing four-course rotation was maintained, spring beans were sown each year and only sugar beet on the root break.

Phosphorus. 39 lb P/acre was applied to all plots not given superphosphate in the past (Treatments 3, 5, 6 and 8); the old rate was increased slightly to 19·5 lb P/acre and was continued on Treatments 4, 7, 9 and 10. The change was intended to discover how quickly yields from very P-deficient soil could equal those from plots given P annually for 65 years and containing nearly enough P residues for maximum yields. The accumulation of fresh P in these poor soils from the new manuring was measured by soil analysis.

Potassium was given only to those plots given it previously but the dressing was increased to 93 lb K/acre. Cereals and beans had responded only slightly to K in the 65 years, and sugar beet not at all. The larger crops grown from 1966 removed more K and the new test was planned to see for how long crops yielding reasonably could obtain adequate potassium from the soil. (There is no other long-term experiment in Britain on soil with a reputation for releasing much K where this information can be obtained.) The dressings and treatment symbols were: P_1 = 19·5 lb P, P_2 = 39 lb P, and K = 93 lb K per acre.

Nitrogen tests were modified as experience accumulated. 'Nitro-Chalk' was used instead of sodium nitrate. Initially 56 (N_1) *v.* 112 (N_2) lb N/acre was given for non-leguminous crops, the smaller dressing to Treatments 4, 5, 6 and 7, where N was not given before. For spring-sown crops, dressings were applied to the seedbed, for winter wheat they were given in March. In each year the test on beans was of none *v.* 56 lb N/

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acre (on N_2 treatments). In 1967 large losses of nitrate were measured in drainage water during May, and extra top-dressings of 28 lb N (N_1 treatments) and 56 lb N (on N_2 treatments) were given to barley on 15 June and to sugar beet on 18 July. From 1967, 56 lb N/acre was given to FYM-treated plots for the three non-leguminous crops. In 1968, 112 lb N/acre was given to all the N-treated plots of wheat, barley and beet; on N_2 treatments this was followed by a top-dressing of 56 lb N/acre, given when tissue-tests on the crops suggested they needed more N. The dressings were given to wheat on 15 May, to barley on 29 May, and to sugar beet on 25 July. In 1969 more detailed work was done on tissue testing and provisions were made for testing two top-dressings. 112 lb N/acre was given to all N-treated plots when sowing spring crops and to winter wheat during late March. Top-dressings of 56 lb N/acre were given to wheat on 28 May, to barley on 3 June and to beet on 3 July, all when plant tissue contained little nitrate. A further top-dressing of 56 lb N was applied for sugar beet on Treatments 3 and 10 on 20 August. Table 6 summarises the new nitrogen manuring treatments.

TABLE 6

Nitrogen manuring used in Rotation I experiment, 1966–69

Treatment number	Symbol	Beans (all years) cwt N/acre	Wheat, barley, sugar beet: 1966 (All non-legumes)	1967 Wheat	1967 Barley, sugar beet	1968 (All non-legumes)	1969 Wheat, barley	1969 Sugar beet
1	FYM(+N)	0·0	0·0	0·5	0·5	0·5	0·5	0·5
3	N_2	0·5	1·0	1·0	1·5*	1·5*	1·5	2·0†
4	N_1	0·0	0·5	0·5	0·75*	1·0	1·0	1·0
5	N_1	0·0	0·5	0·5	0·75*	1·0	1·0	1·0
6	N_1	0·0	0·5	0·5	0·75*	1·0	1·0	1·0
7	N_1	0·0	0·5	0·5	0·75*	1·0	1·0	1·0
8	N_2	0·5	1·0	1·0	1·5*	1·5*	1·5*	1·5*
9	N_2	0·5	1·0	1·0	1·5*	1·5*	1·5*	1·5*
10	N_2	0·5	1·0	1·0	1·5*	1·5*	1·5*	2·0†

* Includes one top-dressing.
† Includes two top-dressings.

Yields

Results with organic manures. The only continuity with the past has been with the bone meal treatment (No. 2) and for three crops; average yields have been:

	Yields, cwt/acre: 1900–19	1900–61	1966–69
Wheat	15·4	14·3	15·4
Barley	11·7	10·7	10·3
Beans	17·5*	15·3	14·1

* 1905–18 only.

Average yields of wheat, barley and beans given bone meal have been nearly the same recently as during the first 60 years. Wheat yields in the last four years were the same as the average in the first 20 years of the experiment, but bean and barley yields were less.

Yields with FYM in 1966–69 cannot be compared with older yields because the dressing has been doubled and 56 lb N/acre was given to the main plots in the last three years.

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The table below sets out the average yields obtained with FYM and with the full fertiliser dressing.

	1900–61		1964–69 'Classical' treatments		1966–69 New treatments	
	FYM†	NPK†	FYM‡	NPK†	FYM‖	N_2P_1K‖
Wheat (cwt)	18·9	19·4	27·5	27·0	35·2	35·2
Barley (cwt)	16·2	18·0	21·8	17·8	28·9	30·3
Beans (cwt)	21·7	20·8	22·5	21·9	24·7	21·3
Sugar beet (tons)	13·1*	10·0*	12·9	9·2	16·0	15·4

* 1956–65.
† Amounts in Table 1.
‡ 6 tons/acre in 1964 and 1965, 12 tons in later years.
‖ New treatments, including 12 tons of FYM and with 56 lb N/acre on FYM-treated plots from 1967.

During each of the periods, wheat has yielded similarly with FYM and with the NPK dressing. Barley has varied more, yielding a little better with NPK than with FYM except in the continued 'classical' test from 1964–69 which includes four years with double FYM dressings. Beans and sugar beet have yielded consistently more with FYM than with fertilisers during each of the periods.

Results of the fertiliser tests. Table 7 gives yields from the modified experiment. 'Main effects' are summarised in Table 3; only for potassium (with a test of 93 lb K/acre against none) are these normal. The 'main effect' of nitrogen is of double *versus* single dressings in 1966 and 1967, and of seedbed dressings alone *versus* seedbed plus top-dressing in 1968 and 1969. The phosphate test is of a double quantity (P_2 = 39 lb P) to plots not given any before 1965 against half as much (P_1) continued on plots that were dressed annually from 1900 and contained large residues. The complicated interaction effects are not discussed here.

Phosphorus. For all four crops the 'main effect' of P was negative; over the four years, average yields from plots with residues from 65 years of P manuring exceeded those from poor soils given twice as much fresh phosphate. The surprising feature was that giving phosphate to previously starved (P_2) plots quickly increased yields (Table 7). In the first year (1966), Treatment 9 (N_2P_1), which has always received phosphate, yielded more beans, wheat and barley (but a little less beet) than Treatment 3, with superphosphate for the first time. Results in intervening years were variable but wheat, barley and sugar beet yielded better with N_2P_2 than with N_2P_1. Although Saxmundham soil is naturally very deficient in phosphate, the deficiency can be quickly remedied; 39 lb P/acre seems enough for the crops we have grown, both to maintain yields from poor soil and to build up reserves.

Potassium had a much larger effect on wheat in 1966–69 than in any of the preceding periods of the experiment. The effect on beans was also larger than previously, but that on barley and beet was negative; yields of beet were slightly depressed by potassium fertiliser. The results with wheat and beans suggest that potassium reserves in the soil may now be diminishing to the point where K-fertilisers will be generally needed, but this is not supported by the results with barley and beet. The experiment suggests that small K dressings should be used for wheat and legumes on these Chalky Boulder Clay soils, but that other crops need none.

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TABLE 7

Yields of crops grown in Saxmundham Rotation I experiment, 1966–69

Crop			FYM	BM	N_2P_2	N_1P_1	N_1P_2K	N_1P_2	N_1P_1K	N_2P_2K	N_2P_1	N_2P_1K	Mean
Field beans	Grain (cwt/acre)	1966	24·3	7·3	9·1	8·4	7·5	8·8	16·8	15·2	14·3	15·1	12·6
		1967	23·2	17·5	18·8	18·6	17·0	18·8	22·8	22·9	16·3	21·7	19·8
		1968	27·6	23·6	24·5	25·4	25·6	25·8	28·4	27·5	22·0	30·5	26·1
		1969	13·8	8·1	13·2	12·0	14·0	13·7	15·2	15·3	14·9	17·8	13·8
		Mean	24·7	14·1	16·4	16·1	16·0	16·8	20·8	20·2	16·9	21·3	18·1
Winter wheat	Grain (cwt/acre)	1966	18·7	9·9	27·1	19·8	16·7	17·8	20·9	28·3	28·9	32·2	22·0
		1967	45·3	14·0	34·3	27·7	25·9	21·0	29·2	38·8	36·8	35·3	30·8
		1968	48·4	27·8	40·0	41·8	42·6	45·9	42·5	47·6	43·5	42·7	42·3
		1969	28·6	10·0	32·1	27·0	28·8	25·3	28·4	35·1	29·6	30·8	27·6
		Mean	35·2	15·4	33·4	29·1	28·5	27·5	30·2	37·4	34·7	35·2	30·7
Spring barley	Grain (cwt/acre)	1966	34·2	11·2	29·8	25·4	19·5	28·1	28·0	32·4	31·6	29·1	26·9
		1967	24·0	11·8	25·0	16·5	16·2	15·0	20·8	26·4	24·8	24·9	20·5
		1968	34·3	11·8	35·1	38·4	35·7	32·2	30·9	29·7	42·6	37·5	32·8
		1969	23·2	6·4	30·4	20·5	17·6	23·3	20·9	28·6	28·5	29·6	22·9
		Mean	28·9	10·3	30·1	25·2	22·2	24·6	25·1	29·3	31·9	30·3	25·8
Sugar beet	Clean roots (tons/acre fresh matter)	1966	13·5	4·7	13·7	9·6	7·3	9·3	10·4	10·1	11·3	10·1	10·0
		1967	19·2	5·2	15·8	10·8	11·9	10·7	11·7	17·3	17·7	16·3	13·7
		1968	19·7	7·9	16·9	15·3	15·4	15·4	16·2	15·8	16·7	16·8	15·6
		1969	11·6	3·8	17·6	13·2	13·1	15·7	18·2	18·4	17·3	18·5	14·7
		Mean	16·0	5·4	16·0	12·2	11·9	12·8	14·1	15·4	15·7	15·4	13·5
Sugar beet	Tops (tons/acre fresh matter)	1966	5·8	2·8	6·9	3·9	3·9	3·8	4·2	6·4	7·4	6·0	5·1
		1967	6·0	2·1	6·1	4·0	3·7	3·9	3·9	6·2	7·6	6·5	5·0
		1968	13·6	3·9	15·7	10·3	9·3	9·6	11·0	14·6	16·2	16·0	12·0
		1969	5·0	2·3	17·5	5·9	7·5	10·5	11·4	17·6	18·1	18·6	11·5
		Mean	7·6	2·8	11·5	6·0	6·1	6·9	7·6	11·2	12·3	11·8	8·4
Sugar beet	% Sugar	1966	16·5	15·9	17·3	17·1	17·1	17·2	17·6	17·4	17·6	17·7	17·2
		1967	17·3	17·0	16·8	17·0	18·4	17·3	17·6	17·3	16·7	17·5	17·3
		1968	16·2	15·8	15·6	16·2	16·6	16·3	16·4	15·7	15·3	15·5	16·0
		1969	19·2	18·4	17·7	19·2	19·7	19·1	19·3	19·0	18·7	18·8	18·9
		Mean	17·3	16·8	16·8	17·4	17·9	17·4	17·7	17·3	17·0	17·4	17·3
Sugar beet	Sugar (cwt/acre)	1966	44·6	15·0	47·5	33·0	25·0	32·1	36·7	35·2	39·8	35·7	34·5
		1967	66·6	17·7	53·0	36·8	43·9	37·1	41·2	59·9	59·3	57·2	47·3
		1968	63·7	25·1	52·8	49·5	51·1	50·0	53·2	49·6	51·1	51·9	49·8
		1969	44·6	13·9	62·3	50·8	51·7	60·0	70·3	69·7	64·7	69·7	55·8
		Mean	54·9	17·9	53·9	42·5	42·9	44·8	50·3	53·6	53·7	53·6	46·8

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Nitrogen. The 1966 test was a simple one of two amounts, results were:

N applied lb/acre	Wheat (cwt)		Barley (cwt)		Sugar beet (tons)	
	Grain	Straw	Grain	Straw	Roots	Tops
56	18·8	12·1	25·2	15·8	9·2	4·0
112	29·1	20·0	30·7	18·8	11·2	6·7

More than 112 lb N/acre might have benefited the wheat, but for barley and beet this amount must have been nearly optimum.

In March 1967, N_1 and N_2 treatments received the same dressings as in 1966. Drainage water contained much nitrate during May and crops became yellow, so top-dressings (shown in Table 6) were given to barley on 15 June and beet on 18 July. Both crops responded quickly. Average yields per acre were:

Seedbed dressing/acre		N_1 56 lb N	N_2 112 lb N
Wheat (cwt)		26·0	36·3
Barley (cwt)		17·1*	25·3*
Sugar beet	roots (tons)	11·3*	16·8*
	tops (tons)	3·9*	6·6*
	sugar (cwt)	39·7*	57·4*

* With extra top-dressings of 28 and 56 lb N/acre to N_1 and N_2 plots.

The large gains from the double dressing suggested that the crops would have benefited from still more N; from their appearance the top-dressings should have been applied earlier and should also have been given to wheat.

In 1968 following 112 lb N/acre to both N_1 and N_2 treatments extra top-dressings of 56 lb N/acre were applied to N_2 plots for wheat, barley and beet; the top-dressings were given when analyses of nitrate-N in the stems of cereals and in petioles of sugar beet suggested they were needed. Spring of 1968 was drier than 1967, rainfall was better distributed and drainage water removed much less nitrate. (Results of the nitrate tests on the plants have been reported previously (*Rothamsted Report for 1968*, Part 1, 49–51).) Maximum yields of wheat and barley grain, and sugar from beet, were obtained with 112 lb N/acre applied in March; the only gain from the extra top-dressing on N_2 treatments was 5 tons/acre more sugar-beet tops.

In 1969 the drains at Saxmundham ran on every day of the year until 20 June and much nitrate was lost in the drainage water. Measurements were again made on nitrate in cereal stems and beet leaf petioles (*Rothamsted Report for 1969*, Part 1, 51–53). Extra top-dressings of 56 lb N/acre tested on N_2 treatments were applied to each crop when nitrate concentrations became small (29 May for wheat, 3 June for barley and 3 July for beet). A further top-dressing on 20 August was tested on two plots of beet when leaf nitrate had again become small. The first top-dressings were justified on all three crops. They increased yields by 4 cwt/acre of wheat, 9 cwt/acre of barley and 5½ cwt/acre of sugar and also gave extra yields of sugar-beet tops. The additional top-dressing to beet was not justified (little rain fell after it was applied). Results of the top-dressings given in 1968 and 1969 are summarised below:

	Yields/acre					
	Wheat, cwt of grain		Barley, cwt of grain		Sugar beet, cwt of sugar	
	1968	1969	1968	1969	1968	1969
Yield with 112 lb N in March/April	43·2	27·4	34·3	20·6	51·0	58·8
Increase from top-dressing						
First top-dressing	0·2	4·5	1·9	8·7	0·4	5·6
Second top-dressing	—	—	—	—	—	1·3

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TABLE 8

Amounts of nutrients (in lb/acre) removed each year by crops grown with 'new' treatments in Rotation I experiment, 1966–69

	FYM	BM	N_2P_2	N_1P_1	N_1P_2K	N_1P_2	N_1P_1K	N_2P_2K	N_2P_1	N_2P_1K	Mean
Nitrogen											
Wheat	68·4	25·1	66·1	50·8	47·7	48·3	51·1	74·6	68·0	70·4	57·1
Barley	53·0	16·2	58·5	40·8	35·3	38·4	41·7	56·9	63·4	58·9	46·3
Beans	116·7	70·9	81·5	83·7	73·0	78·6	105·5	106·0	88·0	103·1	90·7
Sugar beet	100·3	33·0	112·8	68·3	64·8	74·4	77·2	113·2	123·1	113·9	88·1
Total of four crops	338·4	145·2	318·9	243·6	220·8	239·7	275·5	350·7	342·5	346·3	282·2
Phosphorus											
Wheat	13·2	5·2	10·7	9·4	8·8	8·7	10·2	11·5	11·6	12·0	10·1
Barley	12·6	3·6	10·4	9·1	7·2	7·8	8·8	9·5	11·1	10·6	9·0
Beans	14·0	7·3	8·4	8·9	7·0	7·6	11·6	9·5	10·5	12·3	9·7
Sugar beet	19·6	6·9	16·4	14·2	12·8	13·8	16·4	15·3	17·7	18·2	15·1
Total of four crops	59·4	23·0	45·9	41·6	35·8	37·9	47·0	45·8	50·9	53·1	43·9
Potassium											
Wheat	39·2	11·3	25·5	22·7	24·8	20·6	25·0	32·9	24·5	32·2	25·8
Barley	30·2	7·7	23·2	17·8	16·8	18·4	21·3	27·9	23·2	24·6	21·1
Beans	65·4	19·3	20·2	20·7	29·5	23·0	36·3	38·8	19·9	31·6	30·5
Sugar beet	209·0	73·3	160·0	133·3	163·0	142·7	179·6	207·3	162·6	195·1	162·6
Total of four crops	343·8	111·6	228·9	194·5	234·1	204·7	262·2	306·9	230·2	283·5	240·0
Calcium											
Wheat	7·9	2·9	8·1	6·6	5·7	5·8	6·0	7·0	8·3	7·9	6·6
Barley	7·8	2·2	7·7	5·9	4·6	5·0	6·0	7·6	8·8	6·8	6·2
Beans	28·2	11·7	14·5	14·4	14·4	14·4	19·8	20·0	16·1	17·8	17·1
Sugar beet	42·5	22·2	52·9	45·4	47·7	51·0	51·2	56·1	61·8	57·6	49·0
Total of four crops	86·4	39·0	83·2	72·3	72·4	76·2	83·0	90·7	95·0	90·1	78·9
Magnesium											
Wheat	5·3	2·0	4·3	3·5	3·4	3·4	3·9	4·7	4·7	4·6	4·0
Barley	4·8	1·5	4·6	3·9	3·2	3·5	4·0	4·4	5·0	4·6	3·9
Beans	5·1	2·8	3·3	3·3	3·1	3·3	4·0	3·9	3·6	3·8	3·7
Sugar beet	23·5	9·0	25·6	17·2	18·0	20·2	19·2	22·2	26·0	23·0	20·4
Total of four crops	38·7	15·3	37·8	27·9	27·7	30·4	31·1	35·2	39·3	36·0	32·0
Sodium											
Wheat	1·9	0·3	0·9	0·7	0·7	0·6	0·7	1·0	1·0	1·0	0·9
Barley	1·5	0·4	2·3	1·0	0·8	1·0	0·9	1·4	2·5	1·5	1·3
Beans	7·2	8·0	13·3	9·5	3·9	8·8	7·5	8·4	13·5	10·5	9·1
Sugar beet	31·0	12·0	89·8	33·6	23·6	43·1	36·4	67·1	98·0	64·0	49·9
Total of four crops	41·6	20·7	106·3	44·8	29·0	53·5	45·5	77·9	115·0	77·0	61·2

The four years' results emphasise the difficulties of using nitrogen fertiliser, even in an old-established and carefully controlled experiment. In 1966 the two amounts given to the seedbed did not show how much N was needed for maximum yield, or whether applying part of the N as a late top-dressing would have benefited the crop. In 1967 and 1969 much nitrate was leached during short periods of large rainfall in April and May; other experiments on the field showed later top-dressings were much more efficient than seedbed dressings, provided there was enough rain to wash them in. In 1967 the need for extra dressings was realised too late for them to be fully effective. In 1969 the top-dressing for barley was applied at the beginning of June just as three weeks of dry weather started, and the fertiliser remained on the soil surface. By contrast, in a spring with well-distributed rainfall, such as 1968, little nitrate is lost from seedbed dressings and timing of the N-dressing is of little importance.

Nutrients removed. Table 8 gives average amounts of nutrients removed annually by the crops grown with new treatments. P_1 dressings supplied 19½ lb P and P_2 39 lb P/acre/year; the K dressing supplied 93 lb K/acre. The nutrients supplied by 12 tons of FYM were twice those shown in Table 1. Annual changes in N, P and K calculated from Table 8 are in Table 9. No balance has been calculated for nitrogen except for Treatments 1 and 2. The FYM added from 1966–69 supplied more N than the crops removed. On the bone meal-treated plot, yields are limited by N-deficiency and, on average, all crops except beans have recovered little N from natural sources if all the N in bone meal becomes available. Fertilisers given to the other treatments have, on average, supplied about twice as much N as harvested crops recovered.

TABLE 9

Estimates of annual changes in nutrients in soils of Rotation I experiment with modified manuring, 1966–69

Treatment number	Treatment	Annual changes (lb/acre)		
		N*	P	K
1	FYM + N	+152	+55	+35
2	Bone meal	−18	+34	−27
3	N_2P_2	(−80)	+28	−57
4	N_1P_1	(−61)	+9	−49
5	N_1P_2K	(−55)	+30	+34
6	N_1P_2	(−60)	+29½	−51
7	N_1P_1K	(−69)	+7½	+27
8	N_2P_2K	(−88)	+27½	+16
9	N_2P_1	(−86)	+7	−58
10	N_2P_1K	(−86)	+6½	+22

* Data for N are balances for Plots 1 and 2; but for Plots 3–10, they are amounts removed by crops.

Phosphorus. The crops removed only about 50% to 70% of the smaller dressing given to P_1 treatments (depending on the amount of N given). With the double dressing but without P during the classical period, only about a quarter was recovered by the crops (these statements take no account of P recovered from the soil). The crops on plots given phosphate each year from 1900 always contained more P (on average 7 lb P/acre more in the four years) than crops on plots given their first dressing in 1965–66. About 5 lb P/acre/year accumulated as residues from the small dressing during the classical period; the crops now grown leave about 7 lb P/acre from the slightly larger P dressing

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given since 1965. The double dressing provides nearly 30 lb P/acre/year more than the crops use, and this residue is accumulating in the soil.

Potassium supplied exceeded the total amounts removed by crops during the four years, and from 20 to 40 lb K/acre are accumulating annually (the amount depends on the N dressing applied). Although there was little yield response to K-manuring, crops on K-treated plots contained 57 lb K/acre in the four years more than crops without K-fertiliser. The largest amount of K removed from soil by crops receiving no K fertiliser was about 230 lb/acre in four years. Increasing the nitrogen dressings in the new treatments has increased the maximum K extracted annually from 42 lb/acre during the 'classical' period to 58 lb of K during the last four years. With full NPK manuring from 1900 to 1965, potassium has not accumulated on Treatment 10 (Table 5); the manuring now used on this plot leaves a residue of about 22 lb K/acre annually.

Analyses of the soils

The soils of each plot were sampled in 1957 and the analyses described by Cooke *et al.* (1958). Later samplings were in spring 1966 (after the experiment had been ploughed about 10 inches deep in winter 1965), and in summer 1969. Analyses are in Table 10.

The soils have reserves of calcium carbonate and pH is not altered by treatment.

Organic carbon is most in FYM-treated plots; differences caused by other treatments are small but largest values were in plots given most fertiliser and where crops were largest. The plots were ploughed about 5 inches deep until 1964, and twice as deep since. The subsoil ploughed up diluted the old top-soil so that all percentages of organic matter and nitrogen are less in the 1969 than in the 1957 samples. Total phosphorus in the 1957 samples reflected the balance between P applied by manuring and removed by crops. With the continued classical manuring on the sub-plots, deeper ploughing has obliterated much of these differences between the fertiliser-treated plots. There has been an apparent loss of total P in the ploughed layer of the P-treated plots but not on those without P presumably because the subsoil was as rich in total P as the top-soil of these untreated plots. The only large differences remaining are that both FYM and bone meal have left much more total P in the soil than has superphosphate. The diminution in total P caused by deeper ploughing is smallest on FYM-treated plots, presumably because organic phosphorus from FYM had already been leached into the subsoil (P under FYM-treated plots moves similarly at Woburn and Rothamsted (Warren & Johnston, 1961)).

Comparing the 1969 samples from the large plots given 'new' treatments with those from small sub-plots continuing the old treatments shows there was little effect on total P contents from four years of phosphate manuring (P_2) to previously untreated plots. However, the new dressings considerably increased bicarbonate-soluble P and, already, there are only relatively small differences between P_1 and P_2 treatments. The new manuring has similarly increased P concentrations in equilibrium with 0·01 *M* calcium chloride solutions.

Exchangeable potassium still reflects the accumulations of K added by FYM, or K-fertilisers, and differences caused by the larger crops produced with N and P treatments and smaller ones without these nutrients. On plots where exchangeable K had accumulated during the classical period, deeper ploughing has diminished the amounts. On plots not given K-fertiliser (Treatments 3, 4, 6 and 9), the exchangeable K changed little between 1957 and 1969, presumably because the newly-incorporated subsoil was as rich in K as the surface soil. Potassium soluble in 0·01 *M* calcium chloride solution also shows

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TABLE 10

Compositions of the soils of Rotation I experiment

(Values are averages for four plots)

Plot			1	2	3	4	5	6	7	8	9	10	Mean
Classical treatment 1900–69			FYM	BM	N	P	K	O	PK	NK	NP	NPK	—
Modified treatment 1966–69			FYM + N	BM	N_2P_2	N_1P_1	N_1P_2K	N_1P_2	N_1P_1K	N_2P_2K	N_2P_1	N_2P_1K	—
Sampling	Date	Area											
$CaCO_3$ %	1969	New	0·74	1·10	1·12	1·12	1·48	1·07	0·80	0·74	0·73	1·16	1·01
pH (in water)	1969	New	8·0	8·2	8·1	8·1	8·1	8·1	8·0	8·0	8·1	8·1	8·1
Organic carbon (Walkley–Black values, uncorrected) %	1957	Classical	1·55	1·01	0·92	0·99	0·95	0·94	1·01	0·95	1·04	1·01	1·04
	1965/66	Classical	1·38	0·77	0·77	0·79	0·74	0·79	0·82	0·80	0·82	0·84	0·85
	1969	Classical	1·32	0·78	0·72	0·75	0·72	0·75	0·75	0·73	0·79	0·83	0·82
	1969	New	1·22	0·77	0·71	0·71	0·67	0·70	0·70	0·72	0·75	0·76	0·77
Total N, %	1957	Classical	0·199	0·149	0·136	0·139	0·137	0·135	0·142	0·139	0·146	0·144	0·147
	1965/66	Classical	0·192	0·127	0·122	0·120	0·121	0·124	0·132	0·130	0·130	0·130	0·132
	1969	Classical	0·193	0·132	0·123	0·133	0·117	0·118	0·128	0·128	0·128	0·135	0·131
	1969	New	0·175	0·127	0·125	0·116	0·121	0·115	0·126	0·127	0·126	0·122	0·128
Total P, %	1957	Classical	0·071	0·088	0·042	0·056	0·041	0·042	0·056	0·041	0·056	0·056	0·055
	1965/66	Classical	0·065	0·065	0·040	0·048	0·036	0·037	0·048	0·036	0·049	0·046	0·047
	1969	Classical	0·068	0·073	0·045	0·049	0·040	0·043	0·048	0·036	0·049	0·050	0·050
	1969	New	0·066	0·068	0·045	0·050	0·043	0·042	0·046	0·040	0·045	0·046	0·049
P soluble in 0·5*M* $NaHCO_3$ ppm	1957	Classical	33	8	3	23	2	2	20	2	21	19	13
	1965/66	Classical	29·9	8·1	6·0	20·5	8·1	5·4	20·8	6·5	19·3	20·1	14·5
	1969	Classical	41·8	7·7	2·9	21·1	2·7	3·0	22·9	3·4	20·6	25·8	15·2
	1969	New	31·4	5·9	11·7	15·6	10·9	9·4	14·5	12·1	15·3	17·6	14·5
P in equilibrium in 0·01*M* $CaCl_2$ solution μM/litre	1957	Classical	6·3	0·2	0·1	1·6	0·1	0·1	1·1	0·1	1·4	1·0	1·2
	1965/66	Classical	4·0	0·6	0·5	1·0	0·5	0·4	1·2	0·5	1·1	1·2	1·1
	1969	Classical	3·5	0·4	0·3	0·7	0·2	0·1	0·7	0·3	0·6	0·8	0·7
	1969	New	2·1	0·4	0·5	0·5	0·4	0·4	0·6	0·5	0·5	0·6	0·6
K exchangeable, ppm	1957	Classical	268	109	124	116	235	137	180	205	110	154	164
	1965/66	Classical	285	114	118	122	192	129	156	181	111	138	154
	1969	Classical	264	125	115	121	182	138	168	179	113	162	157
	1969	New	242	121	126	123	187	141	169	189	115	157	157
K soluble in 0·01*M* $CaCl_2$ solution, ppm	1965/66	Classical	13·4	4·0	3·9	4·1	7·5	4·4	6·0	7·4	3·4	4·8	5·9
	1969	Classical	11·4	3·0	2·9	3·1	5·6	3·6	4·8	5·2	2·7	4·8	4·7
	1969	New	8·0	2·8	2·9	2·9	5·6	3·2	5·0	5·9	2·9	4·2	4·3
Mg exchangeable, ppm	1965/66	Classical	218	117	124	122	117	119	105	124	105	104	125
	1969	Classical	189	107	95	91	103	95	86	97	84	88	103
	1969	New	169	109	102	99	111	112	94	93	78	82	105

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clearly how K has accumulated on FYM-treated plots and the differences between plots with and without K fertiliser.

Exchangeable magnesium has been considerably diminished by deeper ploughing. Magnesium fertiliser is not applied, so supplies in the top-soil are maintained by rainfall, by crops residues and by weathering of clay. Amounts in FYM-treated plots are still much larger than in fertilised plots. Exchangeable magnesium has clearly been influenced by yields of crops grown during the classical period; amounts are least where N and P fertilisers gave satisfactory yields.

Soil analyses related to nutrient balances. Figures 1 and 2 relate bicarbonate soluble-P and exchangeable-K with the nutrient balance shown in Table 5. (These calculations replace the earlier balance sheet for P and K by Cooke *et al.* (1958), which was based on assumed crop compositions. The satisfactory agreement between exchangeable K, and K balance of Fig. 2 in our paper, and that in Fig. 1 of the earlier one, justifies attempts to calculate such balance sheets even when local analyses do not exist.) Values for soluble-P in the plots are in two groups, plus the isolated point provided by the FYM-treated plot. The relationship appears to be linear; if losses of P in crops are exactly balanced by fertiliser additions, the soils will contain 10 ppm of sodium bicarbonate-soluble P.

There is a good linear relationship in Fig. 2 between the calculated balance for K (additions *minus* losses) and exchangeable K in the soils. If fertiliser additions exactly balance losses in crops, the soils will contain 160 ppm of exchangeable K. Johnston (1969) found that, when losses and gains were balanced in the Broadbalk experiment at Rothamsted, the soils had a similar amount (about 150 ppm) of exchangeable K.

Batey (1964) analysed samples of soil taken before fertilisers were applied in March 1963. (The results were expressed in ppm of P and K in the soil extract.) Amounts of free

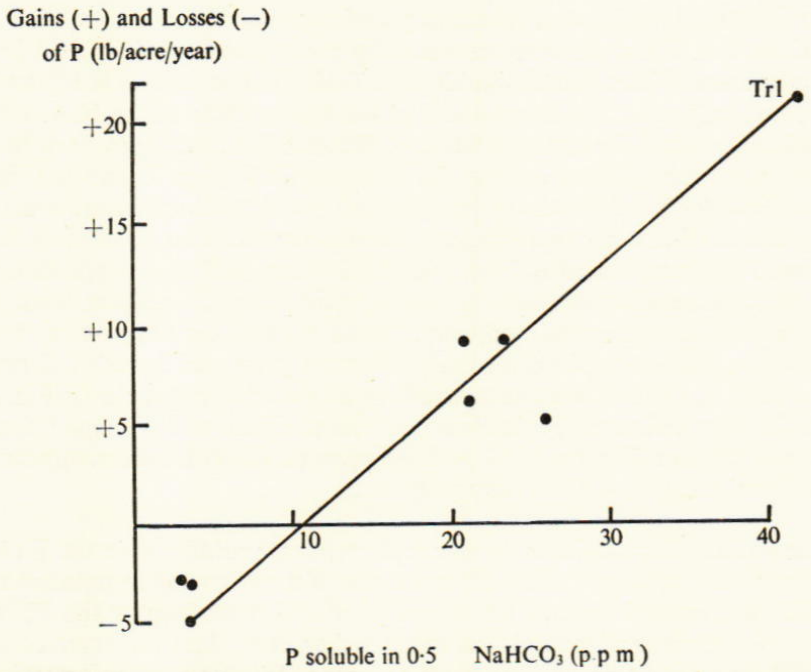

Fig. 1. Relationship between losses and gains of phosphorus and soil P soluble in sodium bicarbonate solution; 1899–1969.

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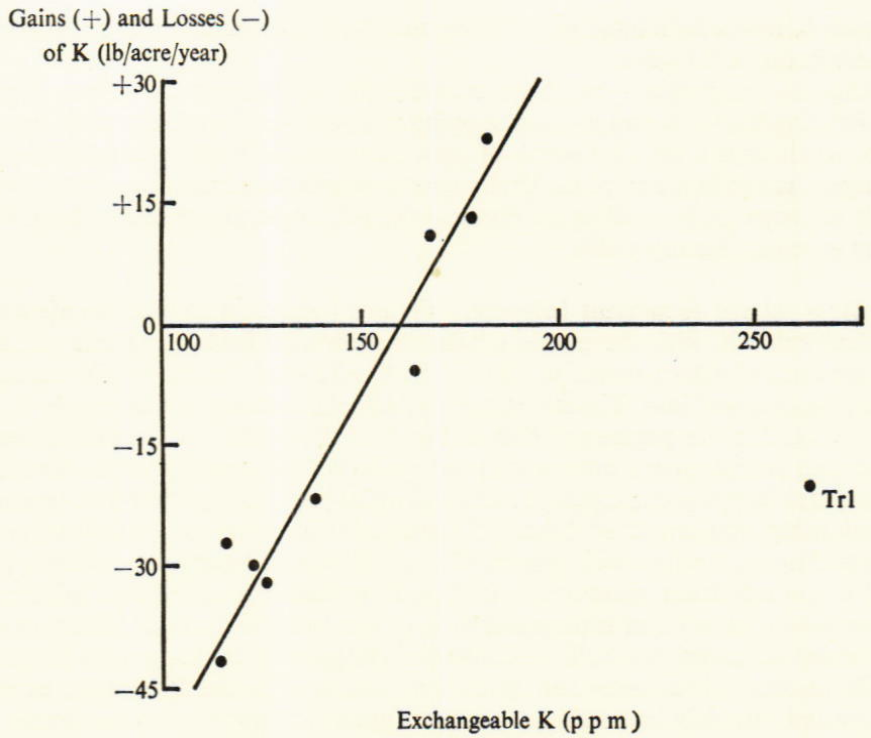

Fig. 2. Relationship between losses and gains of potassium and exchangeable K in the soils; 1899–1969.

calcium carbonate, pH values and percentages of organic matter were similar to values in Table 10. Soluble P and K were measured by the methods used in 1964 in advisory work in England and Wales. Exchangeable K in Table 10, and soluble K by the N.A.A.S. method, were closely related, but soluble P in the soil extracts of the N.A.A.S. method was less well related to bicarbonate soluble P. Because these methods have been widely used, Batey's values are plotted against the balances for P (Fig. 3) and K (Fig. 4). The N.A.A.S. method for P differentiated less clearly than the sodium bicarbonate methods between groups of differently treated plots. Results for the bone meal plots fit satisfactorily in Fig. 3 but are excluded from Fig. 1. Sodium bicarbonate solution does not dissolve bone meal residues whereas the slightly acid N.A.A.S. reagent does. However, in this experiment the bone meal supplied so little N that it is not possible to estimate how valuable the residues are. Relationships between gains and losses of K and Batey's values for soluble K (Fig. 4) were as satisfactory as with exchangeable K (Fig. 2). When losses in crops were balanced by fertiliser additions, Figs. 3 and 4 suggest that the soil extracts would contain 28 ppm of K and 1·5 ppm of P, both values appear to be in Batey's 'medium' category for advisory purposes.

Potassium in FYM. Figures 2 and 4 share a discrepancy; soluble K in the FYM-treated plots is not related to analyses of soils from the rest of the plots and to potassium balance. Either FYM has greatly increased the solubility of soil potassium or the FYM applied during most of the classical period was much richer in K than the samples used from 1964 to 1968 on which this balance sheet is based. We have no information on the composition of FYM used and no evidence except Oldershaw's (1941) statement that

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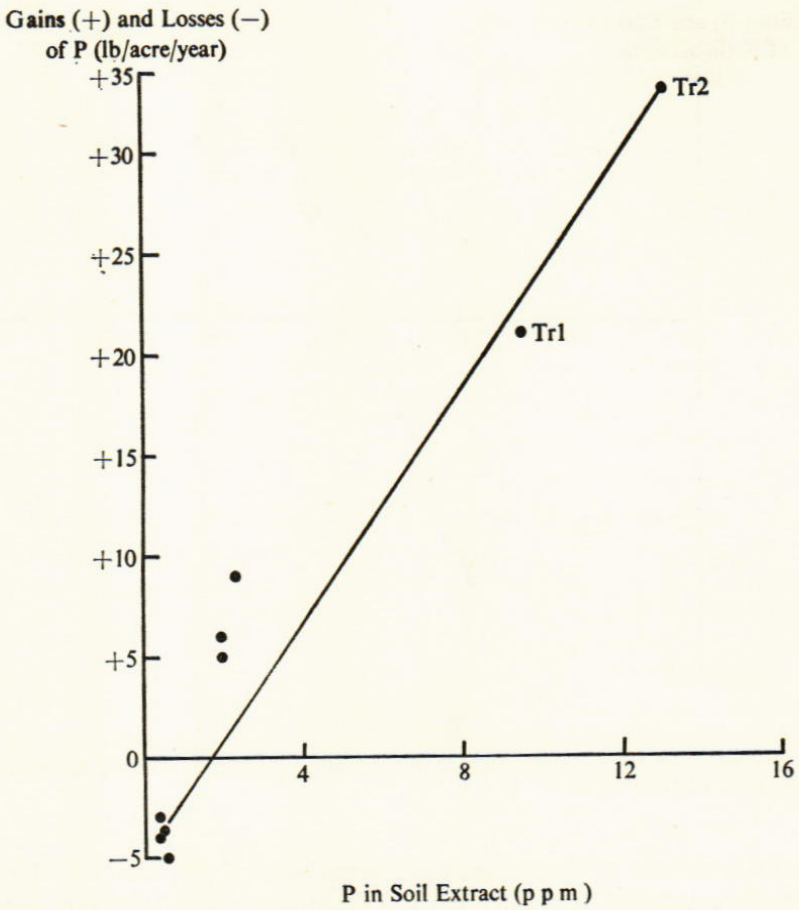

Fig. 3. Relationship between losses and gains of phosphorus and soluble P in soil extracts measured by Batey's (1964) method; 1899–1962.

it was made by fattening bullocks in a covered shed. He said the bullocks did not have a rich cake diet but the FYM made was not removed from the shed until it was applied to the plots. The recent samples used were from dairy stock and were stored in heaps out of doors and their compositions are similar to those of much FYM used in Rothamsted experiments. The earlier Saxmundham manures were completely protected from loss of K by the leaching that occurs during outdoor storage and they may have been much richer in K. Many authors record that some samples of FYM have 4–5% K in dry matter—twice the value assumed here. Extrapolation of the linear relationship in Fig. 2 shows that soluble K would be as found if FYM supplied each year 80–90 lb K/acre more than crops removed (Fig. 4 suggests a similar amount). To supply so much would require FYM with more than 6% K in dry matter (an improbable, but not impossible, value).

Soil differences between blocks. Trist and Boyd (1966) found consistent differences in yield of barley and roots from block to block. Average yields from Block D (Plots 1–10, Fig. 1 of their paper) were about 10% above the mean of the four blocks whereas Block B (Plots 31–40) tended to give smaller yields. Block D also gave the most wheat. These

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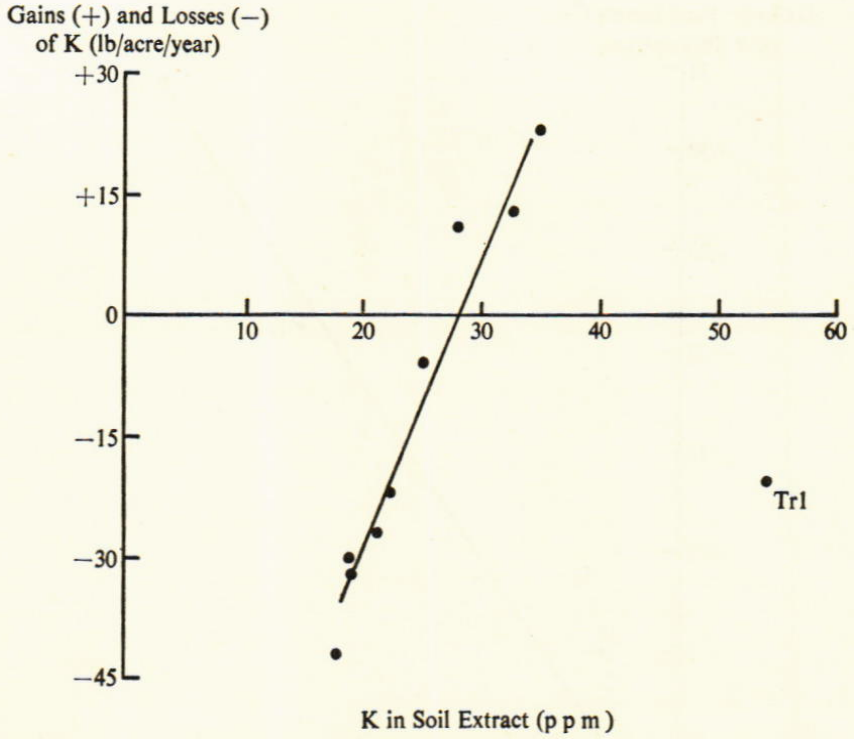

Fig. 4. Relationship between losses and gains of potassium and soluble K in soil extracts measured by Batey's (1964) method; 1899–1962.

fertility trends from east to west affect the comparisons of treatments in the systematic layout; they were ascribed to permanent soil factors, probably depth of the ploughed layer. Table 11 gives average values for blocks of most of the measurements listed in Table 10. There are no large differences that clearly account for better yields from Block D and poorer yields from B. Soils of Block D contain more nitrogen and organic matter and more soluble P than average, but the differences are small. The only striking difference is the much larger content of $CaCO_3$ in Block B—which gave poorer crops. We think this reflects differences in parent material; borings show the subsoils of Block B to be more compact and more gleyed than subsoils of other blocks. The common subsoil in Block B is unaltered typical Boulder Clay, blue-grey, compact and rich in $CaCO_3$.

TABLE 11

Average values of soil properties in blocks of Rotation I experiment (1969)

	Block				
	A	B	C	D	Mean
Nitrogen, %	0·132	0·127	0·123	0·130	0·128
Organic carbon, %	0·78	0·77	0·72	0·81	0·77
Total P, ppm	493	528	464	486	493
$NaHCO_3$-soluble P, ppm	14·7	14·7	13·5	15·2	14·5
Exchangeable K, ppm	154	169	153	151	157
Exchangeable Mg, ppm	105	119	102	95	105
Calcium carbonate, %	0·82	1·87	0·85	0·49	1·01

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On other blocks, subsoils are more open and have weathered more deeply; although all blocks are irregular, better subsoils are more common in blocks A and D than in B and C.

Some analyses were made of subsoil 9–18 inches deep. Subsoil of Plot 4 in Block A contained only 1% $CaCO_3$ (the topsoil had 0·8%); subsoils of five plots in Block B had from 3½ to 19% $CaCO_3$ with a mean value of 11% (the topsoil had 1·9%). Subsoils of Block C, above Block B, had little $CaCO_3$ (from 0·04 to 5·1% and a mean value of 1·3%).

Nutrients supplied by rainfall

Nutrients in rain. Rain samples were collected continuously by a polythene gauge 6 ft above the soil at Saxmundham between 1966 and 1970; 41 separate batches were analysed without filtering. The nutrients supplied annually were:

	lb/acre
NH_4–N	8·4
NO_3–N	6·1
P	0·2
Cl	43
SO_4–S	16
K	2·6
Na	24
Ca	12
Mg	3·7

The nitrogen in rain made an appreciable contribution to the needs of crops not given N fertiliser, but P and K supplied was unimportant. The sulphur suffices for a crop rotation of this kind; the large amount of chloride is quickly leached out (balanced by calcium).

Calcium, magnesium and sodium. The other nutrient cations in rain, Na, Ca and Mg have not been discussed previously. Table 4 gives the amounts in crops grown with the classical manuring and Table 8 with the new fertiliser treatments.

Calcium. Much more calcium was removed by beans and sugar beet than by cereals. Annual removals from fully fertilised plots averaged only about 20 lb/acre from 1900–65 and a little more during the recent period. These losses in crops are much less than is leached annually from this calcareous soil—270 lb/acre (Williams, 1971).

Magnesium. Half or more of the magnesium removed in the four-year rotation was taken by the sugar beet crop (Tables 4 and 8), and the total amounts removed were influenced mainly by the effect of fertilisers in increasing yields of beet. During the classical period, about 7 lb Mg/acre/year was removed, only twice as much as rain supplied and half as much as was lost by leaching. FYM-treated crops usually contained more Mg than fertiliser-grown crops. The manure recently used has averaged 0·7% Mg in dry matter; a 6 ton/acre dressing will have supplied 20 lb Mg/acre/year. The soil of FYM-treated plots contains nearly twice as much exchangeable Mg as plots treated with NPK fertiliser; but the fertilised plots with 80 ppm of exchangeable Mg contain much more than the 30 ppm usually thought to indicate a deficient soil.

Sodium. Cereals contained very little sodium, and beans usually from about 5 to 20 lb Na/acre. Sugar beet contained much more; the average for crops grown with 'new' treatments was 50 lb Na/acre/year. Table 9 shows how sodium removed depends

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on yield but much more on manuring with potassium. Where K was supplied as FYM, or as fertiliser, much less sodium was taken up by beet than where it was not supplied. FYM itself supplied little Na (about 10 lb/acre in a 6 ton dressing). Most Na was removed by crops with the N_2P_1 treatment, when the sugar beet alone contained about 100 lb Na/acre. This is much more than the annual supply of 20 lb Na/acre in the rain. Sodium may not be readily leached and may accumulate in exchangeable forms that can be used by beet; probably the soil also contains a reserve that is slowly released by weathering, because drainage water removes about 30 lb Na/acre/year (Williams, 1971).

Weather and soil conditions at Saxmundham

All previous accounts of the Saxmundham Experiments have stressed the difficulties of working the soil and that good yields depend on good weather. Unseasonable rainfall has had very bad effects on yield. Oldershaw (1941) stated 'In spite of the fact that the district is one of the driest in England, this heavy land is frequently in so wet a state that neither horses nor men can walk on it'. Rainfall has been recorded at Saxmundham for many years but no other weather data until 1965 when we installed instruments to measure temperature, wind, radiation and evaporation with the hope of assessing more precisely the effects of weather on yields.

Oldershaw (1941) and Trist and Boyd (1966) described the drainage of the field and the method of working the plots in 'stetches', with furrows between to remove surface water. A major difficulty with shallow ploughing was that heavy rain was not absorbed quickly enough; the frequent surface run-off washed soil down the field; soil analyses showed that richer soil from some plots must often have washed diagonally across the

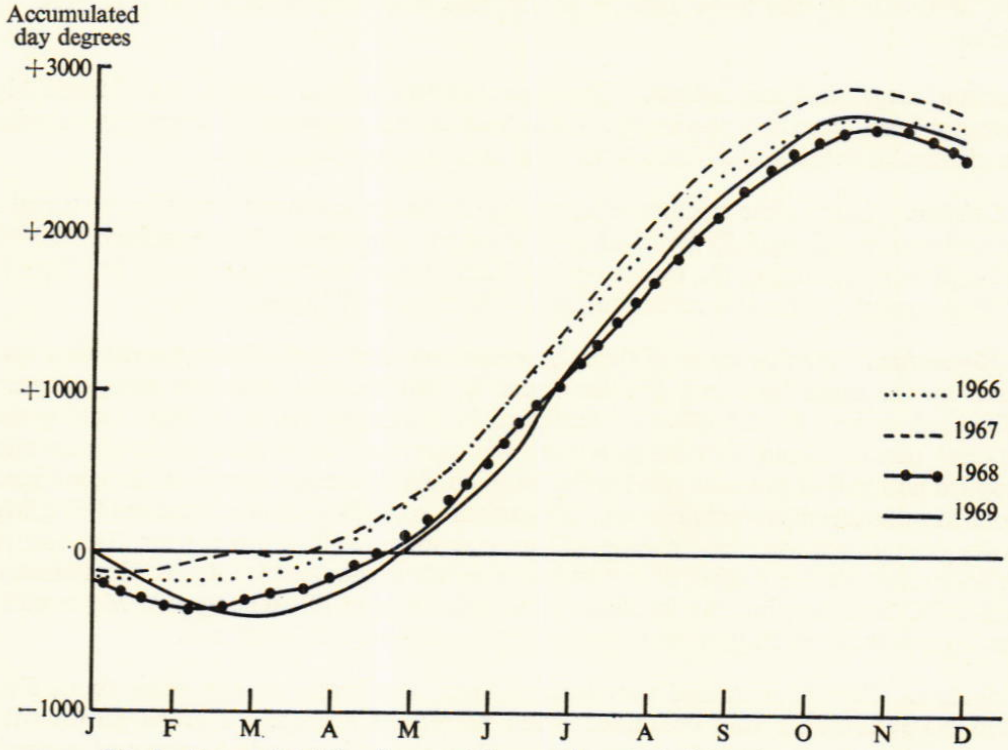

Fig. 5. Accumulated day degrees at Saxmundham for individual years, 1966–69.

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field to contaminate the upper parts of other plots. (After these enriched areas had been recognised they were always discarded at harvest.) To get better drainage, the whole field was mole-drained during autumn 1964, and was then ploughed 10–12 inches deep. Ploughing since has been about 10 inches deep. These measures improved drainage and penetration of rain, and water now rarely stands on the surface except in wheel tracks; surface run-off and erosion have stopped. But the deeper ploughing has introduced other problems. It has often been difficult to get a good seedbed for wheat because the deep furrow slices could not be broken up, especially in dry autumns such as 1969. Because the soil does not readily weather (except on the surface) to give good and deep structure (a major difference from Rothamsted soil), spring seedbeds have often been unsatisfactory, with fine material overlying the massive clods formed by ploughing the previous autumn. Sometimes clods seem to remain unchanged for two or more years; ploughing simply turns them over. These cloddy conditions below the surface no doubt aid drainage during wet summers but they must interfere seriously with the supply of water and nutrients during dry weather.

Temperature. Temperatures in individual seasons are conveniently summarised by showing accumulated daily temperatures above or below 42°F (below which there is very little crop growth). 'Growing Degree Days' (=GDD) (sometimes called 'Heat Units') can be read from tables (Meteorological Office, 1965) or calculated from $GDD = \Sigma(\bar{T} - T_b)$ ($\bar{T}$ is average daily means of maximum and minimum temperatures; T_b is the base temperature selected). In the early part of the year GDD are negative and the time when they become positive is a measure of the earliness of the season; the size of negative values indicates the severity of late winter. Figure 5 gives values for 1966 to 1969. The dates when GDD have exceeded zero have ranged at Saxmundham from late March (1967) to the beginning of May (1969). The two earliest and warmest years were 1966 and 1967; 1968 was a late season and much cooler than the other years. In spite of this, all crops yielded more in 1968 than in the other years (Table 7); beans were 8 cwt/acre, wheat 12 cwt/acre, barley 7 cwt/acre and beet 2 tons/acre more than the average. This remarkably consistent result cannot have been caused by favourable temperatures. 1968 was most unusual in that the *average* wheat yield in Rotation I experiment (42 cwt) almost equalled the *best* yield (43 cwt) in the Rothamsted Ley Arable Experiments (*Rothamsted Report for 1968*, Part 1, 250–252); in other years Rothamsted yields have been nearly twice those at Saxmundham.

Rainfall. Tables 12 and 13 summarise annual rainfall at Saxmundham over the last 40 years. 1965, 1966, 1968 and 1969 were all wetter than average. 1964 was very dry (6 inches less rain than average); yields of wheat and barley were close to average, only sugar beet being checked by drought (Table 2). This seems to illustrate dry weather favouring Saxmundham cereals when the soil was shallowly cultivated. 1967 was also drier than average; in the classical tests wheat yielded more and barley less than average, beet about average (Table 2). In the 'new' experiment (Table 7) beans, wheat, and beet yielded near to average for the four years, and barley less. (Barley yields in Rotation II experiment seem to depend much less on weather than those in Rotation I experiment. Mattingly, Johnston and Chater (*Rothamsted Report for 1969*, Part 2, 91–112) report that the *best* yields in Rotation II experiment between 1965 and 1970 varied only between 34·3 and 37·4 cwt/acre.)

In 1969, 43% of the total year's rain fell in May to August (the average is about 33%). Yields of wheat, barley, and beans were all much less than average, but beet yields were

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TABLE 12

Annual rainfall at Saxmundham 1930–69 (inches)

Year	Total annual rainfall	Mean monthly rainfall	Percentage of annual rainfall		
			Jan –Apr	May–Aug	Sept –Dec
1930	30·32	2·53	18·8	40·9	40·4
1931	24·65	2·05	35·0	38·8	26·2
1932	23·33	1·94	28·0	40·9	31·1
1933	21·21	1·77	23·8	28·3	47·9
1934	21·29	1·77	29·8	29·9	40·4
1935	27·46	2·29	26·2	27·8	46·0
1936	27·63	2·30	30·7	29·9	39·4
1937	19·02	2·42	43·7	24·9	31·4
1938	19·60	1·63	21·5	28·6	49·9
1939	34·61	2·88	32·0	21·3	46·7
Mean	25·91	2·16	28·9	31·1	39·9
1940	23·02	1·92	35·7	19·7	44·6
1941	23·26	1·94	40·2	37·4	22·4
1942	25·26	2·10	27·0	24·3	48·7
1943	19·45	1·62	30·4	27·1	42·4
1944	22·87	1·91	23·7	23·3	53·0
1945	20·25	1·69	27·7	38·6	33·7
1946	29·65	2·47	21·0	43·5	35·5
1947	19·29	1·61	39·7	29·9	30·4
1948	22·00	1·83	27·4	42·1	30·5
1949	18·11	1·51	23·9	27·9	48·2
Mean	22·32	1·86	29·7	31·4	38·9
1950	22·21	1·85	28·7	31·7	39·6
1951	27·69	2·31	49·0	20·9	30·1
1952	27·14	2·26	23·6	29·3	47·1
1953	17·56	1·46	20·8	45·2	40·0
1954	30·71	2·56	21·3	45·4	33·3
1955	25·54	2·13	23·5	38·6	37·9
1956	26·73	2·23	30·1	29·9	40·0
1957	25·44	2·12	26·4	37·3	36·3
1958	31·17	2·60	24·4	46·7	28·9
1959	18·06	1·50	25·5	25·5	49·0
Mean	25·22	2·10	27·3	35·0	37·6
1960	33·82	2·82	22·4	28·5	49·1
1961	24·59	2·05	27·8	26·5	45·7
1962	20·23	1·69	27·3	32·9	39·8
1963	23·52	1·96	32·7	36·5	30·8
1964	18·94	1·58	36·7	39·1	24·2
1965	27·92	2·33	25·7	35·1	39·2
1966	29·22	2·43	24·4	36·7	38·9
1967	23·84	1·99	26·2	31·1	42·7
1968	27·08	2·26	26·0	34·2	39·8
1969	27·58	2·30	30·5	43·3	26·2
Mean	25·67	2·14	28·0	34·4	37·6
1930–69 range	17·56–34·61	1·46–2·88	18·8–49·0	19·7–46·7	22·4–53·0
1930–69 mean	24·78	2·07	28·5	33·0	38·5

a little larger. Presumably weather affects yields of cereals and root crops differently. (There has been no difficulty in growing nearly 20 tons/acre of sugar beet and potatoes (much more than national averages) in the modified Rotation II experiment.)

Table 14 shows monthly rainfall. The good year, 1968, was drier than average in March, April and May, but then rainfall was close to average until August. The disas-

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TABLE 13

Monthly rainfall Saxmundham 1930–69 (inches)

Years		Jan	Feb	Mar	Apr	May	June	July	Aug	Sept.	Oct.	Nov	Dec
1930–39	Range	0·52–5·38	0·32–3·71	0·30–2·85	0·70–3·62	0·34–3·56	0·04–2·76	1·01–4·42	0·40–4·73	1·28–5·86	0·75–8·35	0·95–4·67	0·70–3·81
	Mean	2·30	1·78	1·33	2·18	2·09	1·44	2·56	1·90	2·93	2·73	2·78	1·89
1940–49	Range	0·98–4·10	0·41–2·93	0·31–3·50	0·70–1·78	0·12–2·28	0·41–3·59	0·85–4·31	0·54–4·49	0·24–2·96	0·49–4·30	0·98–5·22	1·15–3·43
	Mean	2·33	1·38	1·62	1·22	1·34	1·66	2·01	2·06	1·75	2·19	2·62	2·11
1950–59	Range	0·42–5·13	0·20–3·76	0·00–3·61	0·10–4·19	0·20–2·90	0·30–3·58	0·84–2·72	1·75–5·63	0·00–3·14	0·72–5·87	0·50–4·71	1·00–3·48
	Mean	2·15	2·04	1·37	1·39	1·63	2·20	1·92	3·16	1·95	2·46	2·79	2·16
1960–69	Range	0·65–3·52	0·64–2·87	0·71–3·19	0·94–3·72	0·44–3·61	0·30–3·65	0·85–4·54	1·20–3·49	0·06–5·44	0·28–7·57	0·91–3·91	0·67–3·39
	Mean	2·02	1·51	1·62	1·90	1·86	1·74	2·56	2·63	2·34	2·55	2·64	2·29
1930–69	Range	0·42–5·38	0·20–3·76	0·00–3·61	0·10–4·19	0·12–3·61	0·04–3·65	0·84–4·54	0·40–5·63	0·00–5·86	0·28–8·35	0·50–5·22	0·67–3·81
	Mean	2·20	1·68	1·49	1·67	1·73	1·76	2·26	2·44	2·24	2·48	2·71	2·11

TABLE 14

Saxmundham rainfall (1964–69)

inches (5 inch gauge)

Month	1964	1965	1966	1967	1968	1969
January	0·65	1·83	2·30	1·62	2·50	1·95
February	0·90	1·00	2·06	1·54	2·37	2·87
March	3·19	1·87	0·71	0·83	1·11	2·18
April	2·22	2·47	2·07	2·26	1·05	1·40
May	1·10	1·57	1·64	2·76	1·66	3·61
June	3·65	2·23	2·56	0·75	2·21	1·53
July	1·45	3·05	3·32	1·08	2·52	3·91
August	1·20	2·96	3·20	2·83	2·87	2·89
September	0·29	5·06	0·51	2·83	5·44	0·06
October	2·08	0·37	4·31	2·85	1·99	0·28
November	0·91	2·12	3·39	2·85	1·60	3·91
December	1·30	3·39	3·15	1·64	1·76	2·99
Total	18·94	27·92	29·22	23·84	27·08	27·58
Mean	1·58	2·33	2·43	1·99	2·26	2·30

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trously wet September came too late to affect yields but may have caused the land to be consolidated when ploughed during autumn, so laying the foundation for poor crops of cereals and beans in 1969. In 1969 there was also nearly double the average rain in both May and July; August was also wet. These conditions seem to have injured cereals and benefited beet.

A wet August in 1965 was followed by double the average rain in September; this wet period may have damaged soil structure so that the yields of following beans, wheat and beet in 1966 were much less than average, as happened for cereals and beans in 1968–69. By contrast, 1967 (with near average yields (except for barley)) did not have extreme rainfall in any month; March, June and July were dry and the autumn had near to average rainfall, which seemed a good preparation for satisfactory yields in 1968.

These general comments do not show how temperature and rainfall affect crops yields. Interactions of rainfall and soil structure are undoubtedly important but have not been defined. A moderately dry autumn that permits satisfactory ploughing seems important, as is a spring that permits satisfactory seedbeds to be prepared. We have already commented on the difficulties of using N-fertiliser efficiently at Saxmundham. 1968 was singular, for there was no heavy rainfall during spring to leach early dressings, and later rain was enough for May top-dressings to be used efficiently. Probably intensity and distribution of rain in spring are as important as total amount, and their effect on leaching has been discussed (Williams, 1971).

Seasonal variations in nitrogen in cereals. Nitrogen contents of cereals are important in assessing quality; they have differed considerably during the four years with the new treatments. Average values for crops on all treatments were:

	%N in dry matter			
	Wheat		Barley	
	Grain	Straw	Grain	Straw
1966	1·65	0·42	1·50	0·48
1967	1·62	0·23	1·80	0·49
1968	1·79	0·45	1·58	0·61
1969	1·80	0·46	1·40	0·46

The two crops were affected differently by season. When per cent protein was largest in barley in 1967 it was least in wheat; the converse was true in 1969.

Future work

The experiments at Saxmundham have given excellent opportunities for extending work on P and K to soils with very different characteristics from those at Rothamsted; we have made good progress with valuing phosphate residues in Rotation II experiment and with measuring potassium release in Rotation I. Long-term experiments on the two farms also measure the productivity of the two soils. Some comparisons are in Table 15. By increasing nitrogen fertiliser and testing amounts of N, P and K fertiliser, the crops grown in Rotation I during the last three years were not limited by nutritional deficiencies easily remedied by fertilisers. Except in 1968, cereals and beans grown with our best manuring have yielded much less than crops at Rothamsted; wheat in 1966 and barley in 1967, yielded no more than national averages (Table 15). Cereal yields at Woburn also exceeded those at Saxmundham except in 1968. No crop of wheat or barley at Saxmundham yielded nearly as much as the largest amounts usually harvested at Rotham-

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TABLE 15

Comparisons of yields obtained at Saxmundham, Rothamsted, Woburn and nationally

		National average yields	Best yields		
			Saxmundham	Rothamsted	Woburn
Wheat (cwt of grain)	1966	32·4	32·2	58	43
	1967	30·6	45·3	66	53
	1968	33·3	48·4	40	34
	1969	28·2	35·1	66	44
Barley (cwt of grain)	1966	29·9	34·2	55	51
	1967	29·8	26·4	56	46
	1968	30·1	42·6	39	33
	1969	27·4	30·5	49	41
			R I / R II		
Sugar beet (tons of roots)	1966	14·9	13·5 / —	20·8	23·3
	1967	14·6	19·2 / 19·6	21·1	18·1
	1968	14·9	19·7 / —	22·1	19·9
	1969	15·2	18·5 / 21·2	19·3	16·7
Potatoes (tons of tubers)	1966	10·6	— / 20·5	21·4	13·5
	1967	10·2	— / —	22·5	10·6
	1968	10·5	— / —	16·4	13·7
	1969	10·1	— / 19·2	17·0	17·2
Beans (spring) (cwt of grain)	1966	—	24·3	31	—
	1967	—	23·2	30	—
	1968	—	30·5	21	—
	1969	—	17·8	25	—
Lucerne (cwt of dry matter)	1968	46 (hay)	113·4 (2nd year)	85·4	—
	1969	—	109 (3rd year)	34·1	—
Temporary grass (cwt of dry matter)	1968	37 (hay)	136 (2nd year)	100·1	104
	1969	37 (hay)	119 (3rd year)	64·2	72

sted during the last ten years; besides being small, cereal yields at Saxmundham also varied widely—as they do at Woburn.

Sugar beet growth in 1966 was checked by a bad seedbed prepared from wet soil, and by waterlogging during summer; yield was less than the national average. In the other three years, beet yielded well, nearly as much as at Rothamsted, and in two years better than at Woburn. Potatoes yielded as well at Saxmundham in 1966 and 1969 as at Rothamsted, and much better than at Woburn. Table 15 shows best yields from the second and third years (1968 and 1969) of lucerne and temporary grass leys and compares them with best yields of corresponding crops on the other farms. Saxmundham yields were much larger, especially in 1969.

These differences between the performance of crops show how difficult it is to develop 'soil productivity ratings' or land use classifications. Cereals are usually rated as easy crops to grow well and roots as difficult; the reverse seems true at Saxmundham. Herbage crops also yielded well in old experiments. Oldershaw (1941) concluded his account of the arable crop experiments by pointing out that Saxmundham land is very similar to an enormous area of boulder clay in various parts of England which was difficult to cultivate; much had gone derelict and become covered with thorn bushes between 1920 and 1940. He said the land was especially suitable for herbage crops. 'Red clover has given as heavy crops as on really good land, . . . tares and lucerne have proved very productive . . . temporary leys have given heavier crops than are often obtained from rich old meadow land'. He recommended temporary leys for hay, silage or seed, followed by a few years of arable cropping.

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After 1969 harvest, when both wheat and barley that were well-fertilised and free from root disease yielded badly for reasons we could not identify, we decided to put the experiment under herbage crops. The plots were split across the middle, the upper half was sown with lucerne, the lower half with a mixture of grasses that will receive much N fertiliser. The classical manuring will continue on the sub-plots which were also sown with grass. There are two purposes. We hope that several years of herbage crops will improve soil condition so that, after ploughing, good cereals may be grown. The large yields of herbage crops we hope to obtain will remove much more P and K from the soil than would mediocre cereals; this change will therefore speed work on release of potassium and on the solubility relationships of soil phosphate at Saxmundham.

Summary

1. An experiment using a four-course rotation of legume, wheat, roots and barley was made on calcareous boulder clay in East Suffolk. The crops received factorial combinations of N, P and K annually from 1900 to 1965. 35 lb of N, 16 lb of P and 47 lb of K/acre were tested, and extra plots had 4 cwt/acre of bone meal and 6 tons/acre of FYM. These treatments were maintained on small areas from 1965 until 1969. Beans, wheat, sugar beet and barley were grown on one block each year. Yields in 1964–69 were comparable to averages of those before 1960; the 1964–69 crops were analysed to construct an annual nutrient balance relevant to the whole period of the experiment.

2. From 1966 to 1969 new treatments were superimposed on six-sevenths of the area of the old plots; only the test of bone meal was unchanged. Two amounts of N were given, some as late top-dressings in 1967–69. Where P had not been applied before 1965, 39 lb P/acre was given; the old P dressing continued on other plots. Potassium was increased on treated plots to 93 lb K/acre. The FYM dressing was increased to 12 tons, and these plots were also given 56 lb/acre of N.

3. Responses by wheat and barley to N have steadily increased from 1900 to 1969. Phosphate fertilising has always been essential for all crops but recent responses are smaller than earlier ones. Wheat, barley and beans, but not sugar beet, have always given *small* responses to K-fertiliser; in 1964–69 responses were less than previously. The capacity of the soil to release potassium seems not to be diminishing, despite the larger crops now grown.

4. During a four-year cycle the crops have obtained the following amounts of N, P and K from plots not given these as fertilisers: about 200 lb of N (half was fixed by the beans), about 20 lb of P and 160 lb of K/acre (sugar beet removed most K). Phosphorus and potassium removed during 70 years is equivalent to 175 ppm P and 0·14% K in the top soil.

5. Wheat has yielded similarly during each period with the FYM and with the full fertiliser dressing; beans, barley and sugar beet have yielded more with FYM (+N in the last period) than with NPK fertiliser.

6. In the modified experiment, 39 lb P/acre given where P was not given before 1965 gave nearly as large yields as did plots that had always received about half as much. 93 lb K/acre increased yields of wheat and beans but not of barley or sugar beet.

7. At least 100 lb N/acre applied in late March or early April was needed by wheat, barley and beet. These crops benefited from 56 lb N/acre applied as top-dressings in the

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summers of 1967 and 1969, when rain during April/May leached out much nitrate. There was no gain from top-dressing in 1968 with smaller spring rainfall.

8. During the recent period, 12 tons/acre of FYM has supplied more N, P and K than crops removed. About 7 lb P/acre is accumulating annually from the small dressing of P fertiliser and nearly 30 lb P/acre from the large one. K-treated plots receive 20–40 lb K/acre more than crops remove.

9. Soil P soluble in sodium bicarbonate and exchangeable K were linearly-related to the balance of losses (in crops) and gains (from fertiliser). If losses exactly balanced gains, the soils would contain 10 ppm of P soluble in 0·5*M* $NaHCO_3$ and 150 ppm of exchangeable K.

10. With the new treatments, 50–60 lb Ca/acre/year were removed by sugar beet, 20 lb by beans, and 6 lb by cereals. Sugar beet removed 20 lb Mg/acre/year, beans and cereals about 4 lb. Uptake of sodium was increased by giving nitrogen and phosphorus and diminished by giving potassium. Sugar beet removed up to 98 lb Na/acre/year, beans about 10 lb and cereals 1 lb or less.

11. Seasonal differences in yields seem not to be related to differences in air temperatures. Poor yields seem to be associated with: (1) rain during autumn enough to interfere with ploughing and lead to poor soil conditions; (2) rain during spring that leaches much nitrate. Good yields were in years when autumn ploughing and seedbed preparation were done well and when spring and early summer rain was less than usual.

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APPENDIX

Methods of analysis used for crops and soils

Crops

Nitrogen by Kjeldahl digestion using $CuSO_4$ and K_2SO_4 as catalysts and determination by 'Technicon AutoAnalyzer' using Varley's (1966) method modified by adding citrate–tartrate buffer.

Nitrate in fresh plant material by the method of Williams (1969).

Phosphorus by dry ashing with magnesium acetate, solution in dilute HCl, and determination by 'Technicon AutoAnalyzer' using the method of Fogg and Wilkinson (1958).

Potassium by dry ashing and solution in dilute HCl and determination by 'E.E.L.' flame photometer.

Calcium, magnesium and sodium by dry ashing and solution in dilute HCl and determination of Ca and Na by emission spectrophotometry (Salt, 1967), Mg by atomic absorption, with strontium as releasing agent (Elwell & Gidley, 1961), using a 'Unicam' SP.900 flame spectrophotometer.

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Soils

Total nitrogen by Kjeldahl digestion with Cu and Se catalysts (Bremner, 1960).

Organic carbon by the method of Walkley (1935).

Total phosphorus by fusion with sodium carbonate (Mattingly, 1970) and determination by 'Technicon AutoAnalyzer' using the method of Murphy and Riley (1962) with a neutralisation step.

Sodium bicarbonate-soluble P by extraction using the method of Olsen *et al.* (1954) and determination by 'Technicon AutoAnalyzer' using the method of Murphy and Riley (1962) with a neutralisation step.

0·01M $CaCl_2$-P. Extraction by the method of Schofield (1955) and determination with a 'Technicon AutoAnalyzer' using the method of Murphy and Riley (1962).

0·01M $CaCl_2$-K. Extraction by the method of Schofield (1955) and determination by 'E.E.L.' flame photometer.

Exchangeable magnesium and potassium extracted by the semi-micro method of Metson (1956); K by emission spectrophotometry; Mg by atomic absorption using a 'Unicam' SP.900 flame spectrophotometer.

Calcium carbonate by the manometric method of Williams (1948).

pH on a 1 : 2·5 soil : water ratio, using a glass electrode.

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Plan of Saxmundham

A plan of Saxmundham showing the position of the Rotation I experiment is at the end of the volume.

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Long-term Liming Experiments at Rothamsted and Woburn

J. BOLTON

Introduction

Few experiments on the Rothamsted and Woburn farms have been specifically designed to study the effects of liming on crop yields, although both soils are naturally acid and liming has been an integral part of crop husbandry for centuries. Only the permanent grass plots (Park Grass) of the 'classical' experiments include liming treatments. However, liming has been necessary on the permanent wheat (Broadbalk) and barley (Hoosfield) experiments at Rothamsted, and on the Classical cereal plots at Woburn, partly because some fertilisers, especially ammonium sulphate, acidified the soil.

Description of the experiments. In 1962 two liming experiments were started on very acid soils at both Rothamsted (Sawyers) and Woburn (Stackyard), with plots given 0, 2, 4 and 6 tons/acre of ground chalk (<$\frac{1}{8}$ in. mesh; 47% N.V.). Interactions of liming with cumulative annual phosphate and potassium dressings were studied by including superphosphate (0·5 cwt P_2O_5/acre) and potassium chloride (1·0 cwt K_2O/acre) treatments in 4×2^2 factorial designs. There were two replicates giving a total of 32 plots at each site. In autumn 1962 a further 2 tons/acre limestone was given to the plots initially given 6 tons/acre at Rothamsted, and 0·75 and 1·5 tons/acre were given to the plots at Woburn already given 4 and 6 tons/acre.

Both fields had for many years been 'reserved sites' where lime and fertilisers were withheld, to provide soils and experimental sites acid and deficient in phosphate and potassium.

Crops

Spring tick beans (1962–64). 'Gartons 30B' was sown in 1962 and 1963 and 'Gartons Pedigree' in 1964 at 200 lb/acre in rows 21 in. (1962 and 1963) and 10½ in. (1964) apart. Simazine (1·0 lb a.i./acre) was used each year at both sites to kill weeds. Winter beans planted in autumn 1963 at Woburn were so severely damaged by birds that spring beans were resown in early 1964, with a repeated dose of simazine.

Spring barley (1965–67). The variety Maris Badger was used each year in both experiments, sown at 156 lb/acre. Basal nitrogen fertilisers were as follows:

	Cwt N/acre	
	Rothamsted	Woburn
1965	0·50 N/C	0·50 N/C
1966	0·50 N/C	0·50 S/A; 0·50 N/C*
1967	0·75 N/C	0·62 S/A; 0·38 S/A*

N/C = 'Nitro-Chalk' 21% N; S/A = Ammonium sulphate 21% N; * = topdressed.

Potatoes (1968). The variety Majestic was grown with basal dressings of 1·5 cwt N/acre at Rothamsted and 2·0 cwt N/acre at Woburn, given as 'Nitro-Chalk' before planting

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Analytical methods

Soils. Surface soil (0–9 in.) was taken from all plots each autumn except in 1965. The samples were air-dried and sieved (<2 mm). The pH was determined in 1 : 2·5 soil : water suspensions, stirred, left for one hour, then measured using a glass electrode and Pye 'Dynacap' meter. Figure 1 gives mean values of the pHs during the experiments.

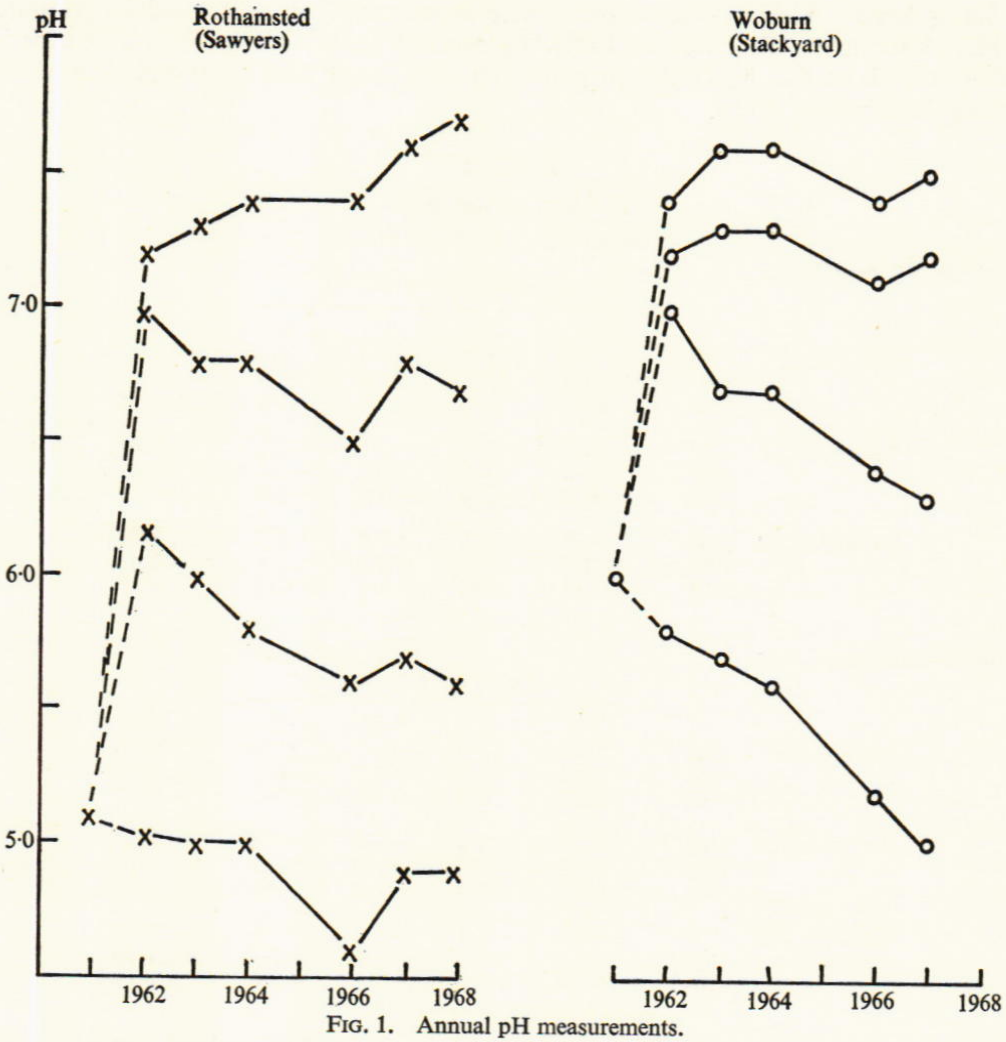

FIG. 1. Annual pH measurements.

The 1967 samples were analysed for exchangeable cations by leaching 2 g of air-dried soil with 75 ml of *N* ammonium acetate at pH 7, using the tube method of Metson (1956). December 1968 samples from the Rothamsted experiment were used to measure 'available' phosphate soluble in 0·5*M* sodium bicarbonate (Olsen *et al.*, 1954).

Crops. The beans grown during 1962–64 were not analysed. Samples of barley grain were analysed each year for the major cations, and, for two years, manganese. Oven-dried grain was ground <0·5 mm and sub-samples were ashed at 450°C for 3 hours.

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The ash was extracted with *N* HCl, and K, Na and Ca measured in the extract by emission and Mg and Mn by atomic-adsorption flame spectrometry. Similar analyses (except Mn) were made on oven-dried potato slices, ground <0·5 mm from each plot.

Results

I. Crop yields

Spring beans. Yields of beans from these experiments were discussed by Moffatt (1967). A summary of the results (Table 1) shows that the optimum pH in both experiments was about 6·8. Responses to potassium were larger than to phosphate and increased in successive crops.

TABLE 1

Yields of spring beans

(cwt grain/acre at 85% D.M.)

Rothamsted—Sawyers

		Limestone tons/acre				
		0	2	4	8	S.E.
Mean yields	1962	12·3	16·0	20·3	18·6	±1·51
	1963	10·7	20·7	23·0	22·5	±1·21
	1964	14·7	19·0	19·8	17·1	±1·26
Response to P	1962	−0·7	−2·5	−1·7	+2·2	±3·01
	1963	+0·8	−3·7	+1·0	+2·8	±2·43
	1964	−0·7	−2·4	+0·2	+1·8	±2·53
Response to K	1962	−2·9	+1·6	+2·5	−0·2	±3·01
	1963	+0·5	+3·2	+2·2	+3·4	±2·43
	1964	−1·0	+4·8	+4·5	+4·8	±2·53

Woburn—Stackyard

		Limestone tons/acre				
		0	2	4·75	7·5	S.E.
Mean yields	1962	14·8	19·0	19·1	22·0	±0·86
	1963	12·4	17·5	16·5	16·5	±0·84
	1964	19·1	16·5	13·0	13·2	±0·57
Response to P	1962	+3·5	−0·4	−0·6	+0·6	±1·73
	1963	+2·5	+3·4	−1·0	+2·3	±1·69
	1964	+1·9	+0·4	+1·2	+1·7	±1·16
Response to K	1962	−0·1	−0·1	−2·2	−3·6	±1·73
	1963	+1·7	+6·4	+3·6	+2·7	±1·69
	1964	+5·0	+7·5	+4·1	+5·0	±1·16

An anomalous result in the final year at Woburn was that liming significantly lessened yields and most grain was obtained from the unlimed plots (pH 5·0). This may have resulted from simazine damaging plants differentially on soils at different pHs. Simazine hydrolyses faster and is adsorbed more strongly in acid than neutral soils and liming has been observed to increase the toxicity of simazine to other crops (Burnside & Behrens, 1961). In 1964, a double dressing (2 lb a.i./acre) was applied, one to the winter crop that failed, another to the spring crop. We now know that 2 lb/acre a.i. of simazine can severely damage bean crops at Woburn (Johnston & Briggs, 1970). Soil samples taken after ploughing from each plot (in November, when the yields were known) were sown

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with mustard, which is sensitive to simazine. The mustard grew equally well in soil from all plots, so the simazine-damage hypothesis was not proven.

There was some evidence that in the same year, simazine damaged the beans at Rothamsted. The crop was shorter at intervals across the plots corresponding exactly to the boom width of the sprayer, indicating damage where the spray from successive swathes across the plots overlapped.

Spring barley. Except from the unlimed plots grain yields were reasonable, exceeding 30 cwt/acre. However they diminished during the three years especially on the most acid plots and without phosphate fertiliser (Table 2). At both Rothamsted and Woburn, the

TABLE 2

Yields of spring barley

(cwt grain/acre at 85% D.M.)

Rothamsted—Sawyers

		Limestone tons/acre				
		0	2	4	8	S.E.
Mean yields	1965	25·9	41·8	41·7	41·3	±3·07
	1966	21·7	35·1	38·0	38·2	±2·31
	1967	11·5	34·5	33·6	30·8	±2·53
Response to P	1965	+3·4	+1·2	+1·3	+1·1	±4·34
	1966	+6·5	+2·4	+2·7	+2·4	±3·27
	1967	+7·6	+7·5	+12·4	+13·8	±3·58
Response to K	1965	−7·4	−1·8	−2·0	−1·2	±4·34
	1966	−7·1	+2·9	+1·2	+4·4	±3·27
	1967	−1·6	+0·5	+6·2	+8·4	±3·58

Woburn—Stackyard

		Limestone tons/acre				
		0	2	4·75	7·50	S.E.
Mean yields	1965	38·0	39·7	42·2	42·4	±0·34
	1966	36·9	39·5	41·0	40·9	±0·45
	1967	29·0	33·5	34·7	35·0	±1·07
Response to P	1965	+4·9	+1·7	+2·1	+2·3	±0·48
	1966	+4·0	+0·8	+1·7	+2·1	±0·63
	1967	+11·8	+8·2	+2·8	+4·7	±1·52
Response to K	1965	−1·0	+0·9	−0·4	−0·5	±0·48
	1966	+0·5	+1·4	−0·2	+0·7	±0·63
	1967	+2·3	+2·6	+4·4	+1·3	±1·52

largest yields (39–43 cwt/acre grain) were from plots with soil pH 6·5–7·5. Without phosphate, yield was largest at pH 7 at Woburn but in two of the years at Rothamsted the best yield was at pH 5·7. The phosphate response increased over the three years because yields without phosphate decreased more than with phosphate. If yields from successive barley crops declined because root-attacking fungi became more prevalent, it seems that applying phosphate lessens their effects.

The experimental errors (Table 2) were much larger at Rothamsted than at Woburn, and an attempt to explain some of the large differences (1 ton/acre) between replicate plots at Rothamsted is described in part III of this paper. Details of liming and fertiliser effects on soil and crop compositions are described in part II.

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Potatoes. In contrast to barley and beans, the yields of potatoes were not affected by soil pH at either site. However, responses to phosphate and potassium fertilisers differed with different dressings of lime (Table 3). At Woburn, the phosphate response was larger

TABLE 3

Yield of potatoes in 1968

(tons fresh tubers/acre)

Rothamsted—Sawyers

	Limestone tons/acre				
	0	2	4	8	S.E.
Mean yield	9·2	10·4	10·7	9·9	±0·70
Response to P	+3·22	+1·76	+1·27	+3·51	±1·40
Response to K	+0·60	+3·89	+4·82	+5·32	±1·40
Interaction PK	+2·17	+3·40	+0·90	−1·40	±1·40
Yield from PK plots	12·2	14·9	14·2	13·6	±1·40

Woburn—Stackyard

	Limestone tons/acre				
	0	2	4·75	7·50	S.E
Mean yield	10·7	10·3	9·6	9·8	±0·36
Response to P	+4·91	+1·83	+2·90	1·97	±0·72
Response to K	+4·03	+6·54	+6·46	+6·37	±0·72
Interaction PK	+1·40	0·00	+1·89	+1·35	±0·72
Yield from PK plots	15·8	14·5	15·2	14·6	±0·72

in unlimed than limed plots and in both experiments the response to potassium was least in the most acid plots, because liming decreased yields when potassium was not given. A similar 'lime-induced potassium deficiency' has been observed with other crops (Adams & Pearson, 1967), and can be explained by liming increasing the proportion of potassium adsorbed on the exchange complex and decreasing the concentration of potassium in soil solution. Potassium ions can displace adsorbed calcium from cation exchange sites on the soil more easily than aluminium, which is the predominant exchangeable ion in acid soils (Black, 1968).

Total yields of tubers from plots given both phosphorus and potassium were similar at Rothamsted and Woburn, and were unaffected by liming (Table 3).

The percentage of ware potatoes (1·5 in. riddle) at Rothamsted was slightly increased by potassium fertiliser, from 94·3 to 97·6%. Plant numbers were unaffected by the treatments. At Woburn also, the only statistically significant effect on the proportion of ware tubers was an increase from 92·8 to 97·4% by potassium.

Effects of fertilisers on the composition of the tubers are discussed later. Experimental errors were larger at Rothamsted than at Woburn, as they were in the previous barley crops, probably for similar reasons.

A noticeable feature of both experiments at harvest was that stoloniferous grasses (mainly *Agrostis gigantea* Roth) were extensive in the very acid plots. The infestation closely followed the plot boundaries. However, some of the most infested plots yielded 8–11 tons/acre of tubers. The sites of both experiments were fallowed in 1969 to control the grass weeds by cultivation.

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Discussion. The pHs giving largest yields of barley and beans broadly confirm previous work. Gardner and Garner (1953) stated that below pH 5·6 both crops grew badly. Adams and Pearson (1967) tabulated maximum pH values at which responses to lime had been observed in southern U.S.A. and Puerto Rico. For barley this was pH 6·0, for potatoes 5·0, consistent with my results. However, there is no 'optimum' pH for each crop under all conditions. Growing plants in nutrient solutions showed long ago that the hydrogen-ion concentration of the growing medium (or soil solution) is '*per se*' unimportant. It is interactions between acids and the soil itself that affect the composition of the soil solution and, consequently, crop nutrition. The most important primary causes of poor growth in acid soils are toxicities of aluminium and manganese and deficiencies of calcium, phosphorus and molybdenum, and it is the relative importance of these in each combination of crop and soil that must be determined (Adams & Pearson, 1967). The most useful results from the experiments described here were on the interactions of liming with phosphorus and potassium nutrition of the crops, especially the phosphorus nutrition of barley and its possible effect on root disease damage, and on potassium nutrition of the potatoes.

There is now ample evidence that different varieties of crop plants, especially of cereals, differ in their response to liming and soil pH. Neenan (1960) showed that some varieties of wheat and barley tolerate much aluminium in the soil and others much manganese. Ikeda *et al.* (1965) suggested a connection between 'acid-soil resistance' and the capacity of barley varieties to withstand phosphorus deficiency, and evidence for this is discussed in part III of this paper.

II. Composition of the crops and soil

Spring barley. Fertilisers usually affect the composition of cereal grain less than straw and in both experiments most observed differences were small. Liming increased phosphorus and magnesium but, unexpectedly, not the calcium concentrations in the grain. The largest effect of liming was on the manganese content, especially in the most acid plots (Fig. 2). Rothamsted barley contained about 6 ppm more manganese than Woburn, with each amount of liming.

Potassium fertilisers slightly increased potassium and decreased sodium in the grain; these are effects observed in most crops, especially in leaves. Potassium fertilisers also increased manganese in the grain (Fig. 2).

Appendix Table A summarises the effects of liming, phosphate and potassium additions on grain composition.

Potatoes. The composition of potato tubers is more sensitive than that of cereal grains to the nutritional status of the soil and the treatments applied gave larger effects (Appendix Table B).

Liming, which increased phosphorus and calcium concentrations in the tubers in both experiments, decreased potassium, especially at Woburn. Sodium and magnesium concentrations were unaffected.

Potassium fertilisers greatly increased per cent potassium in the tubers and, in contrast to leaves of plants, also increased the magnesium content, from 0·06 to 0·08%. They also decreased phosphorus in the tubers.

The only effect of superphosphate was to increase the phosphorus content slightly.

Analyses of the soils. Appendix Table C gives analyses of the soils. Exchangeable sodium and magnesium were unaffected by liming or the other fertilisers. Exchangeable

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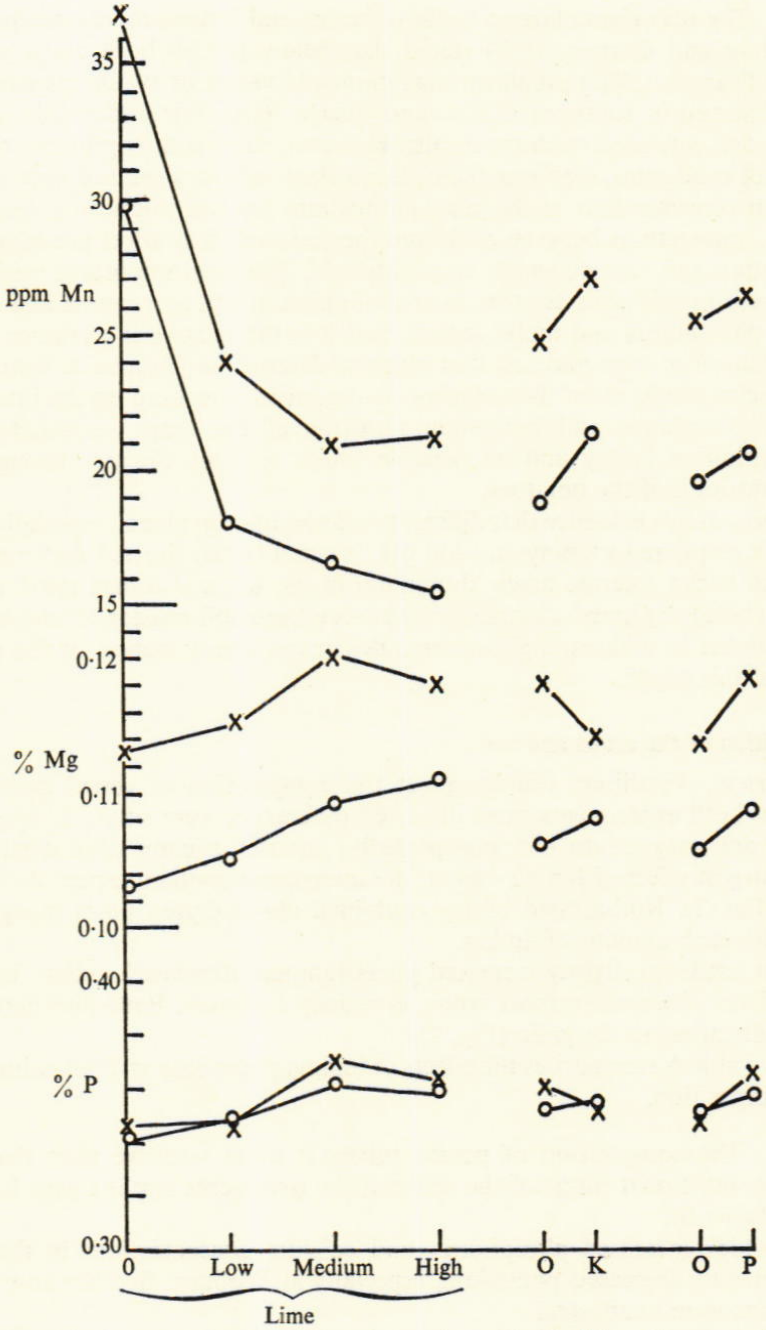

FIG. 2. Effects of liming, superphosphate (P) and potassium chloride (K) on the composition of barley grain, 1965–67. X = Rothamsted; O = Woburn.

potassium was also unaffected by liming but considerably increased by the potassium fertilisers. A balance between changes in soil content and additions and removals of potassium in fertilisers and crops cannot be drawn, because the bean and barley straws were not weighed or analysed.

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Increases in exchangeable calcium in the top 9 in. of the soil were less than the amounts of calcium given as limestone. Apparent lime losses relative to the unlimed plots for each amount of limestone (Table 4) increased as the initial dressing increased

TABLE 4

Estimated annual losses of limestone from the topsoils

(cwt $CaCO_3$/acre)

Rothamsted—Sawyers

	Limestone added, tons/acre				
	0	2	4	8	Mean
1. Using increases in exch. Ca over nil in 1967	—	0·70	1·10	7·15	2·98
2. Using pH changes and pH-exch. Ca graphs	1·95	3·90	1·45	−3·68	1·82

Woburn—Stackyard

	Limestone added, tons/acre				
	0	2	4·75	7·5	
1. Using increases in exch. Ca over nil in 1967	—	1·42	5·55	10·70	5·89
2. Using pH changes and pH-exch. Ca graphs	4·28	6·82	0·00	−0·52	2·64

from 0·7 to 7·2 cwt/acre/annum in the heavier Rothamsted soil and from 1·4 to 10·7 cwt/acre/year in the more sandy Woburn soil. However, these are over-estimates of lime losses because they are based on calcium soluble in *N* ammonium acetate, which dissolves only a proportion of limestone in soils. Unchanged limestone particles were seen in sieved soil from all the limed plots.

A different method of estimating calcium losses from the soil used pH measurements and the relationship between soil pH and exchangeable calcium from the 1967 soil analyses. Graphs of pH changes during the experiments (Fig. 1) show that, with the largest dressing of limestone, the pH at Rothamsted increased with time and that limestone was still reacting with the soil after six years. At Woburn the pH changed little, but had there not been an excess of undissolved limestone, the exchangeable calcium and pH should have become less. This shows that there was still some limestone able to neutralise acidity in the plots in 1968, six years after the dressings were given. Without limestone, acidity increased faster each year at Woburn than at Rothamsted, partly because from 1966 ammonium sulphate was used instead of 'Nitro-Chalk'. This change was made to create a wider range of pHs at Woburn.

Relating changes in pH with the different limings to linear regressions of pH on exchangeable calcium, gives the estimated calcium losses shown in Table 4.

The 'available' phosphate in the Rothamsted soils is discussed in part III.

Discussion. These and other estimates of annual lime losses from different soils and cropping systems (Gardner & Garner, 1953) provide only a rough guide to the need for further liming. Losses of cations by leaching depend not on the amount of drainage *per se* but on losses of the anions, nitrate, sulphate, chloride and bicarbonate. It is therefore the balance between additions and losses of these anions, derived from natural sources or fertilisers, that determine losses of lime and other cations from soils. The type of crop grown, method of husbandry—e.g. whether cereal straw is removed or burnt, amount and type of fertiliser used, and the pattern and amount of rain, are all factors

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affecting lime losses from soils. Because of these variables, regular measurements of soil pH best indicate when further limestone is needed.

III. Causes of heterogeneity in the Rothamsted experiment. A major problem on research farms is to maintain uniformity in fields so that trials can be suitably sited. However, by their nature, experiments create non-uniformity because, to minimise errors, different treatments are given to small areas of land (plots) in close proximity to each other (blocks). The difficulties caused by superimposing fertiliser experiments were shown in the results from the Rothamsted liming experiment.

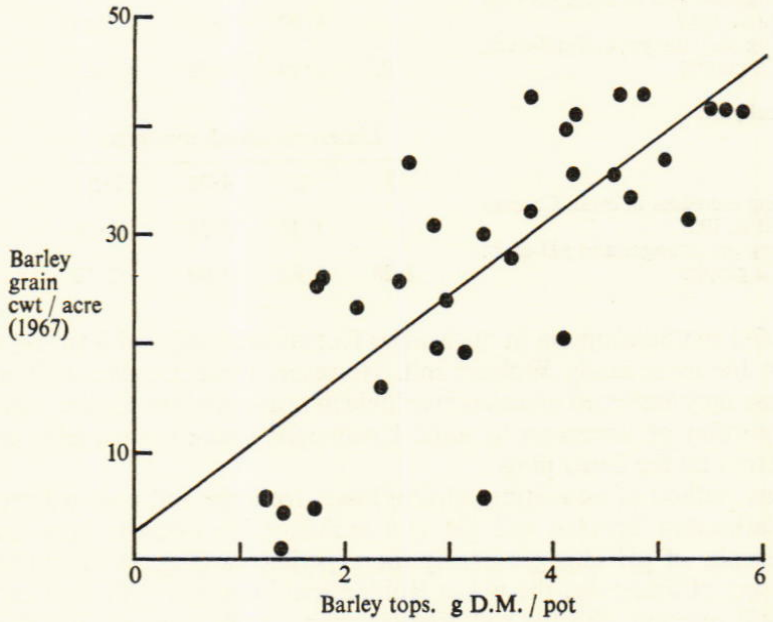

FIG. 3. Relationships between barley yields in the field (grain) and in pots (tops) for each plot of the Rothamsted experiment. ($r = 0{\cdot}77^{***}$).

The mean yields and composition of the barley crops already summarised and discussed disguise large differences between duplicate plots, especially those not given lime. In several pairs of plots differences in yield were more than 1 ton/acre of grain in the final crop of barley. To study the reasons for these differences, soil from each plot was cropped with barley in the glasshouse.

Fresh, undried soil (sieved <6 mm) from each plot was sown with barley (var. Deba Abed) in pots in the glasshouse. Duplicate pots of 2 kg soil were used for each field plot. Basal dressings of 100 mg N/pot were given as ammonium nitrate ten days after sowing. After three months the plants were cut at soil level, dried, weighed and analysed.

Yields of dry matter harvested from the pots were related to grain yields in the field in 1967 (Fig. 3), showing that differences in the field reflected inherent soil properties rather than positional effects, differences in drainage or stoniness—all of which had been considered possible. Therefore, the next step was to identify the factors responsible for differences between the plots, especially of duplicates of a single treatment that differed in the field.

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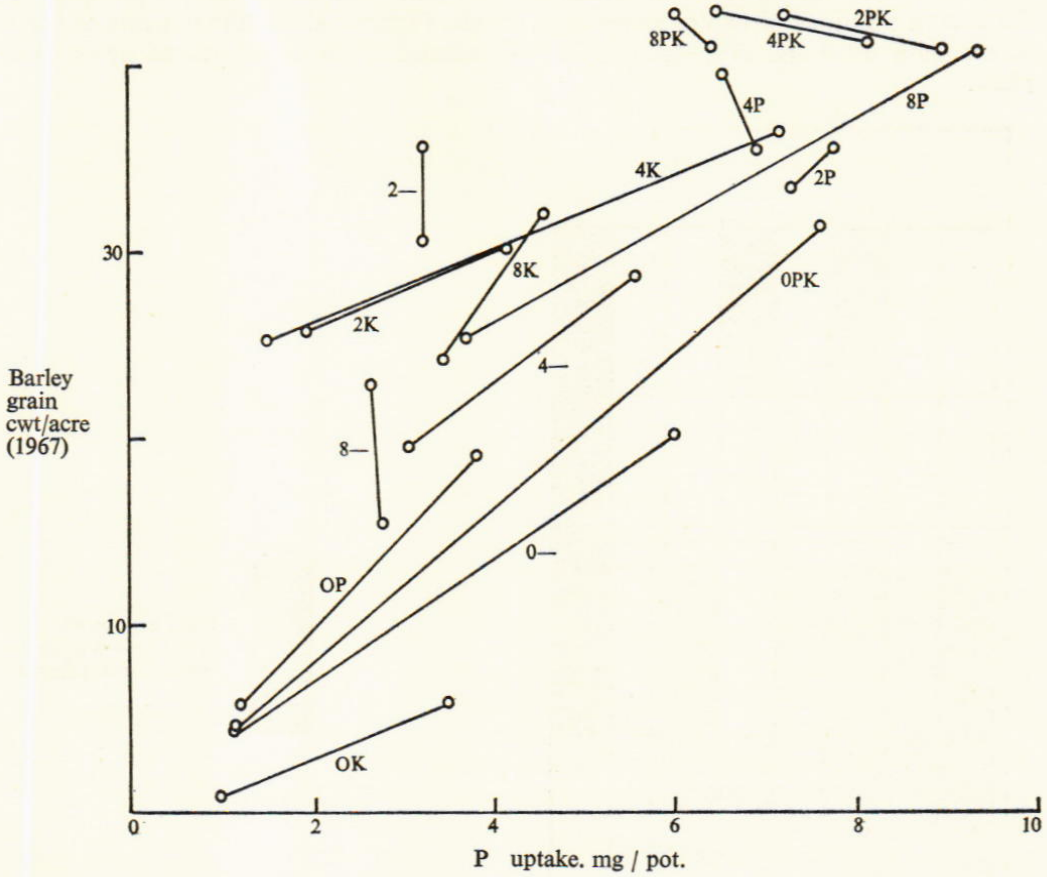

FIG. 4. Relationships between barley yields and P uptake in pots for duplicates of each treatment (numbers = tons/acre limestone; P = superphosphate; K = potassium chloride).

Analyses of barley plants from the pots showed that concentrations of phosphorus in the dry matter most consistently followed the yield differences. Plotting total phosphate uptake in pots against yield of grain in 1967 (Fig. 4) showed that, for each pair of plots, the most P was taken up from the plots that gave most grain in the field, providing this was less than 35 cwt/acre. This was especially so with the seven pairs of plots that differ in yield by more than 7·5 cwt grain/acre (these were the major cause of large coefficients of variation and standard errors in the field experiment). The close correlation between P uptake by the barley in pots and the grain yield in the field ($r = 0{\cdot}804$), confirmed that the differences in yield were associated with the phosphorus nutrition of the barley.

Analyses of soil samples taken in December 1968 (a separate set from those used for the pot experiment) for 'available' phosphate, using the sodium bicarbonate method of Olsen *et al.* (1964), showed large differences between duplicate plots, mostly associated with differences in barley yield. However, there were two anomalies which are discussed later.

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The next step was to relate the distribution of plots with dissimilar soil phosphate to the known positions of two previous experiments. Figure 5 shows the position of these, one made in 1959 and 1961 and one in 1960, relative to the superimposed new experiment.

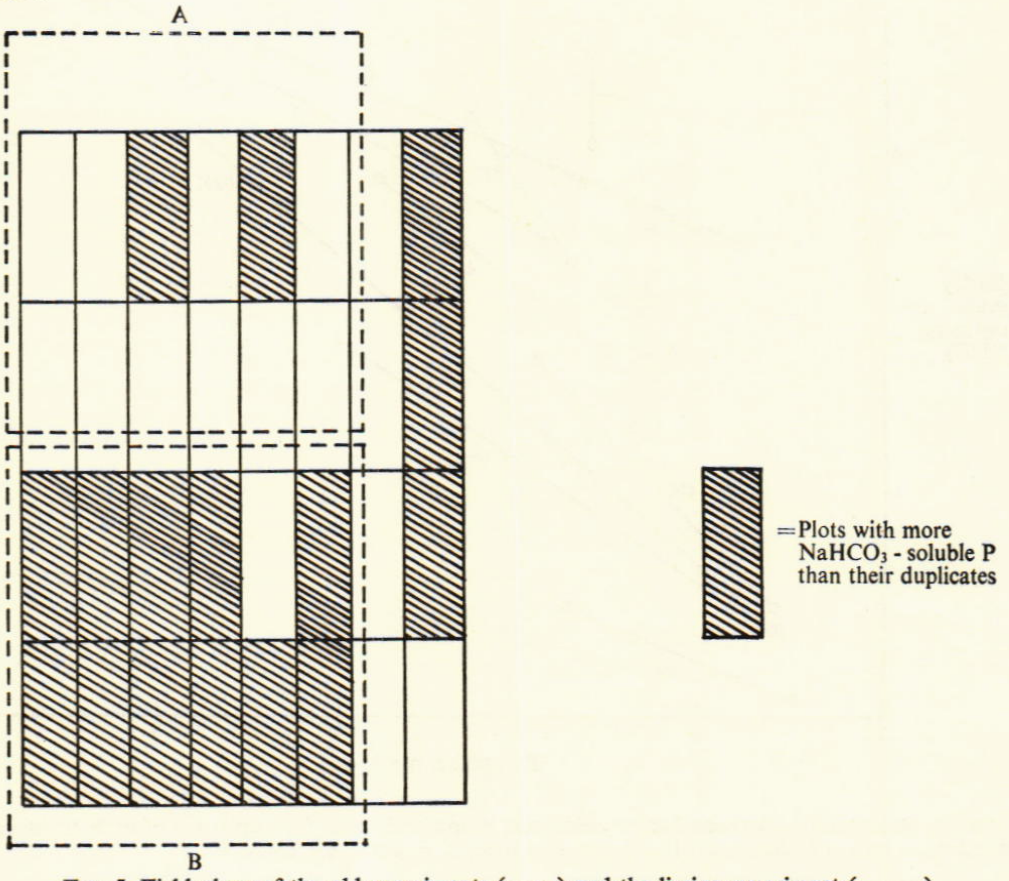

FIG. 5. Field plans of the old experiments (– – –) and the liming experiment (———).

Experiment A testing different forms of K fertiliser on potatoes received a basal dressing of 0·75 cwt P_2O_5/acre in 1960. Some plots received 1·25 and 2·5 cwt K_2O/acre, others none. The same experiment made on site B in 1959 and 1961 was given a total basal dressing of 1·75 cwt P_2O_5/acre, and 0, 2·5 or 5·0 cwt K_2O/acre.

Figure 5 shows that 11 of the 12 plots sited on experiment B contained more 'available' P than their partners. Five of these were among the seven pairs the individuals of which differed in yield by more than 7·5 cwt/acre. This seems to indicate that residual P from the old experiment B could be one cause of large errors in the liming experiment 7 years later.

Discussion. Although the experiments and soil analyses show differences in phosphorus nutrition, it seems improbable these should have such large effects on yield without some other factor operating. The grain yields described in Part I show that the response to superphosphate increased each year especially on the most acid plots, because yields declined without phosphate. The major cause of yield decline in successive cereal crops is the 'take-all' fungus (*Ophiobolus graminis*). Restriction of root growth by this pathogen

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would limit uptake of phosphate more than other nutrients because diffusion over short distances around the root is more important for phosphate uptake than for other nutrients, much of which can be supplied by 'mass-flow' in the transpiration stream (Barber, 1962). Therefore the effect of phosphorus deficiency in the third barley crop could have been accentuated by fungal root pathogens.

TABLE 5

Yield, soil and barley shoot compositions for each pair of unlimed plots

Treatment	Plot Nos.	Soil pH (1966)	$NaHCO_3$-P in soil (ppm)	Exchangeable Ca in soil mg/100 g	Barley yield 1967 cwt/acre	D.M. Barley shoots g/pot	P uptake mg/pot
None	10	4·7	13·0	95	4·1	1·41	1·13
	26	4·8	25·0	123	20·1	4·10	5·99
Superphosphate	1	4·6	19·0	95	5·8	1·23	1·19
	20	4·6	30·0	118	19·1	3·15	3·81
KCl	2	4·5	12·0	95	5·8	3·33	3·50
	29	4·6	22·6	68	0·9	1·42	0·97
KCl plus superphosphate	5	4·5	28·2	80	4·7	1·72	1·12
	23	4·7	23·4	105	31·4	5·23	7·64

Another factor to be considered is the effect of acid soils on phosphorus movement within the plant. The largest difference (26·7 cwt/acre of grain) in yield in 1967 was between plot 5 and plot 23 both given P and K fertiliser but not lime. Table 5 shows that there was more P soluble in $NaHCO_3$ in the soil of plot 5, which yielded poorly, than in plot 23, but P uptake by the barley plants in pots and the %P were considerably less. The main differences between these plots were in exchangeable calcium and pH. Plots 2 and 29 gave similar anomalous results. The more acid soil probably contains more exchangeable aluminium, which can immobilise phosphate in or around roots (Wright, 1943) and induce phosphorus deficiencies in the shoots. Ikeda *et al.* (1965) postulated a relationship between the ability of barley varieties to grow in acid soils and their ability to withstand phosphorus deficiency. My results confirm that barley is very sensitive to factors affecting the movement of phosphorus into the shoots.

Phosphate nutrition was the main factor associated with the large differences in barley yield between duplicate plots in the field experiment. Residues from phosphate dressings given to previous experiments, and differences in acidity between unlimed plots, were major causes of these differences, which in the third barley crop were probably accentuated by 'take-all'.

Summary

The optimum pH for growing spring beans and barley on Rothamsted and Woburn soils was between 6·5 and 7·0, providing phosphate and potassium fertilisers were given. Yields of potatoes were similar at all pH values above 5·0 when phosphate and potassium were sufficient, but when potassium was not given the more acid soils grew larger crops. Yields of beans were increased more by cumulative dressings of potassium than of phosphate (P and K interacted positively). Barley yields were increased more by phosphate than potassium. Potatoes responded most to phosphate on the unlimed soils, whereas response to potassium was largest at pH 7.

Liming decreased manganese, increased phosphorus and magnesium but did not affect calcium concentrations in the barley grain. It increased phosphorus and calcium

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and decreased potassium in the potato tubers. Potassium fertilisers increased the potassium and magnesium concentrations in the potatoes.

Annual lime losses from the soils could not be accurately measured but estimates by two different methods showed they were about 2·5 cwt/acre/annum. The largest amount of limestone continued to increase the pH of Rothamsted soil six years after it was applied.

Large differences in barley yield between replicate plots in the Rothamsted experiment caused unacceptable experimental errors. Similar differences in yields of dry matter of barley grown in pots of soil from each field plot were related to phosphorus uptake. Fertiliser residues from old experiments were one cause of the inconsistency in yield. Accurate recording of the position and treatments given to all plots is essential when fields are re-used for experiments.

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Dr. G. W. Cooke and Mr. J. R. Moffatt started these experiments and I am grateful for permission to reproduce their early results.

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APPENDIX TABLE A

Composition of barley grain

(Mean of three years)

Rothamsted—Sawyers

	Limestone tons/acre 0	2	4	8	Mean	K effect	P effect
				% in D.M.			
K	0·532	0·494	0·510	0·501	0·509	+0·015	−0·002
P	0·346	0·347	0·371	0·363	0·357	−0·008	+0·017
Ca	0·050	0·046	0·046	0·049	0·048	+0·001	0·000
Na	0·019	0·013	0·013	0·015	0·015	−0·006	−0·001
Mg	0·113	0·115	0·120	0·118	0·116	−0·004	+0·005
				ppm in D.M.			
Mn*	37·0	24·0	20·9	21·2	25·9	+2·5	+1·0

Woburn—Stackyard

	Limestone tons/acre 0	2	4·75	7·5	Mean	K effect	P effect
				% in D.M.			
K	0·471	0·465	0·471	0·474	0·470	+0·028	−0·001
P	0·341	0·349	0·361	0·358	0·353	+0·003	+0·006
Ca	0·044	0·044	0·046	0·045	0·045	0·000	0·000
Na	0·010	0·009	0·009	0·009	0·009	−0·004	−0·001
Mg	0·103	0·105	0·109	0·111	0·107	+0·002	+0·003
				ppm in D.M.			
Mn*	29·8	18·0	16·5	15·4	20·0	+2·5	+1·1

* Two years only.

APPENDIX TABLE B

Composition of potato tubers (1968)

Rothamsted—Sawyers

	Limestone tons/acre 0	2	4	8	Mean	K effect	P effect
				% in D.M.			
K	1·72	1·57	1·57	1·57	1·61	+0·71	+0·02
Ca	0·033	0·046	0·042	0·052	0·043	−0·002	+0·002
Mg	0·067	0·066	0·067	0·065	0·066	+0·022	−0·003
P	0·16	0·19	0·21	0·21	0·19	−0·03	+0·02
				ppm in D.M.			
Na	62	65	64	61	63	−4	0

Woburn—Stackyard

	Limestone tons/acre 0	2	4·75	7·5	Mean	K effect	P effect
				% in D.M.			
K	1·64	1·53	1·44	1·42	1·51	+0·67	−0·02
Ca	0·028	0·030	0·031	0·035	0·031	0·000	0·000
Mg	0·072	0·067	0·064	0·067	0·068	+0·022	−0·004
P	0·19	0·19	0·21	0·21	0·20	−0·03	+0·01
				ppm in D.M.			
Na	52	54	52	52	53	−4	−2

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APPENDIX TABLE C

Soil analyses (September 1967)

Rothamsted—Sawyers

	Limestone tons/acre						
	0	2	4	8	Mean	K effect	P effect
pH	4·91	5·66	6·68	7·59	6·21	−0·03	+0·04
Exchangeable K (mg/100 g)	10·9	10·7	10·7	10·7	10·8	+9·0	−0·5
,, Na ,,	1·2	2·5	2·6	2·6	2·2	+0·2	−0·2
,, Ca ,,	97	151	207	272	182	−6	+10
,, Mg ,,	3·1	3·0	3·4	3·0	3·1	−0·2	−0·1
$NaHCO_3$-P* (ppm)	21·6	20·0	22·8	23·4	28·5	−0·1	+12·3

Woburn—Stackyard

	Limestone tons/acre						
	0	2	4·75	7·5	Mean	K effect	P effect
pH	5·03	6·26	7·21	7·53	6·51	−0·10	−0·09
Exchangeable K (mg/100 g)	8·8	8·2	7·8	7·6	8·1	+7·2	−0·4
,, Na ,,	0·9	0·9	1·2	1·2	1·0	−0·1	−0·1
,, Ca ,,	86	132	174	212	151	−10	0
,, Mg ,,	1·3	1·2	1·1	1·1	1·2	0·0	0·0

* Soil sampled in December 1968.

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The Accumulation of Organic Matter in Soil Left Uncultivated

D. S. JENKINSON

Introduction

In the early 1880s, Sir John Lawes allowed two areas of arable land at Rothamsted to revert to wilderness. The site on Geescroft field has been undisturbed ever since and is now an oak-dominated wood. Part of the other site, on Broadbalk field, has also been undisturbed and is now mixed woodland; another part of this site has been stubbed regularly, so that trees did not establish themselves, and is now dominated by a mixed herbaceous vegetation. The botanical changes in these wildernesses have been described at intervals (Lawes, 1895; Hall, 1905; Brenchley & Adam, 1915; Thurston, 1958; Witts, 1965).

Lawes (1895) forecast that the wilderness soils would gain nitrogen, a forecast confirmed by Hall (1905), who sampled both wildernesses in 1904. Soil samples taken from Broadbalk and Geescroft fields during the early 1880s, when the future wilderness sites were still under cultivation, have been preserved, together with those taken in 1904 by Hall. Further samples were taken in 1964 and 1965 and the complete set provides a unique chronosequence of soils for measuring the net rate at which organic matter accumulates in uncultivated land.

Experimental sites, sampling procedure and analytical methods

History of the wildernesses

Broadbalk. The wilderness is on land that had long been in cultivation, possibly since Roman times: the foundations of a Roman temple lie less than 150 m away. A map of 1623 shows that the field now called Broadbalk was then arable. Sometime during the 18th or early 19th century the whole field was chalked, from pits (dell holes) dug down to the underlying chalk, although there are no dell holes in that part of the field now occupied by the wilderness. The site of the wilderness is west of the Permanent Wheat Experiment and carried wheat from 1843 till 1882, like the rest of the field, but was always unmanured (Garner, 1965). The whole field, present wilderness included, was tile drained in 1849. The wilderness site was last cultivated during the autumn of 1881 and the wheat crop sown that autumn was never harvested. Since about 1900, trees and shrubs have been removed by regular stubbing from one part of the wilderness and the stubbings carted off. The present wooded part has been untouched since 1881, save for the felling of some trees along the eastern edge in 1959. In both parts of Broadbalk wilderness, reversion is assumed to have begun in 1883, when the first self-sown crop came up.

Geescroft. Like Broadbalk, this site had long been in cultivation, and is also shown on the 1623 map as arable land. The whole field was tile drained in 1849. The present wilderness was part of an experimental field growing beans from 1847 till 1878, with frequent breaks towards the end because of crop failures. After bare fallowing for four years, clover was grown from 1883 to 1885, and the 'wilderness-to-be' fenced off and left to

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itself in January 1886. It was last cultivated during the spring of 1883. Reversion to wilderness is assumed to start with the clover crop, in 1883.

Soils. Geescroft and Broadbalk wildernesses are 1·3 km apart, on the same gently undulating plateau at an elevation of about 130 m. Both are on very slight slopes and both are on the same soils series (Batcombe). The Batcombe series is classified as a leached brown soil (*sol lessivé*) with a loamy surface layer overlying Clay-with-flints (Avery, 1964). Drainage is somewhat impeded by the clay substratum, as evidenced by varicoloured mottling, black manganiferous deposits, and grey coated cleavage faces at depths below 45–60 cm. Both sites are now classified as moderately well drained. Soil profiles from Geescroft wilderness and from both parts of the Broadbalk wilderness are described in the Appendix. Table 1 shows the mechanical composition of the soils. Mechanical analyses were done on composite soil samples made, for each soil layer, by combining equal weights of fine soil (0·635 cm sieve) from each of the four holes dug per site. The mechanical composition of the stubbed site on Broadbalk is almost identical with that of Geescroft all the way down the profile. Although the 0–22·9 cm layer in both the wooded and stubbed sites in Broadbalk is similar, there is appreciably less clay and more silt in both the 22·9–45·7 and 45·7–68·6 cm layers of the wooded site. This is consistent with the greater thickness of the stony loam layer (see Appendix) in some of the sampling holes of the wooded section. The mechanical analyses of all three profiles are consistent with the suggestion (Avery 1964) that the surface horizon of the Batcombe series contain loessial material. The origin and development of the soil on Broadbalk was discussed in Part 2 of the *Rothamsted Report for 1968*.

Earthworms are very active in both parts of Broadbalk wilderness: both are mull sites and there is no carry-over of leaf litter from year to year. In Geescroft earthworm activity is less and some irregular areas are now covered with a thin moder layer, up to 1 cm thick. In December 1965 eight equispaced quadrats were sited along the 1965 (No P) soil sampling line (see 'Location of Sampling Sites' below): in four the 1965 leaf fall lay directly on the mineral soil, in the others the 1965 fall lay on partly decomposed leaf litter from previous years. Geescroft is in transition from mull to moder: as the pH continues to fall (see Table 3), earthworms will probably disappear from those parts of the site they still occupy and the whole area then go over to moder.

Soil sampling. So that samples taken at different times should be directly comparable, the sampling procedure used in 1881 and 1883 (described in detail by Lawes and Gilbert, 1882) was followed in 1964 and 1965. Briefly, after removal of plants and surface litter, a strong steel box 6 inches (15·2 cm) square and 9 inches (22·9 cm) deep was driven into the ground until the top was level with the soil. The soil and stones in the box were then removed, giving the 0–9 inch sample, the surroundings dug away till level with the bottom of the box, the box again driven down 9 inches and the 9–18 inch sample taken out. Further depths were sampled similarly.

The samples were air dried (25–35°C), and the weights of air-dried fine soil, i.e. soil passing a 0·25 inch (0·635 cm) sieve, stones retained by the sieve, and roots retained by the sieve recorded. From these weights, corrected to an oven-dry basis (24 hours at 100°C), the weights of fine oven-dry soil, stones and roots per hectare were calculated, knowing the area of the sampling box. Samples were stored, air-dry, in sealed bottles. The root weights are subject to large experimental error and will not be considered further: to assess these accurately it would have been necessary to sample much larger volumes of soil, especially in the wooded sites.

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TABLE 1

Mechanical composition of Broadbalk and Geescroft soils

Site	Sampling date	Land use	Sampling depth, cm	As percentage oven-dry fine soil passing 0·635 cm sieve				
				Gravel 6·35–2 mm	Coarse sand 2–0·2 mm	Fine sand 0·2–0·02 mm	Silt 0·02–0·002 mm	Clay <0·002 mm
Broadbalk field	November 1964	Stubbed	0–22·9	4	5	41	22	24
			22·9–45·7	3	4	29	16	45
			45·7–68·6	2	3	26	10	57
Broadbalk field	November 1964	Wooded	0–22·9	3	5	42	22	23
			22·9–45·7	2	5	39	21	30
			45·7–68·6	1	3	28	14	50
Geescroft field	April 1965	Wooded	0–22·9	4	5	44	23	21
			22·9–45·7	3	4	32	17	43
			45·7–68·6	2	4	29	9	55

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The 1904 samples were taken and stored in the same way except that a 0·3 cm sieve was used and a known weight of chalk was picked out of the 0–9 inch Broadbalk samples before sieving. Table 3 gives, for each site and depth, the factors used to convert analyses done on the 0·3 cm soil to a 0·635 cm basis. These factors were obtained by measuring the amount of stones passing a 0·635 cm sieve but retained by a 0·3 cm sieve in the 1964 and 1965 samples and assuming that this weight of stones had been excluded from the corresponding 1904 samples.

Sampling was usually done along a straight line laid across the site to be sampled, and the holes dug at equal intervals along this line. The number of samples taken, i.e. holes dug per site at each sampling, is given in Table 3. For analysis, soil was ground to pass a 30 mesh sieve.

Location of sampling sites

Broadbalk. No soil samples taken before 1895 from what is now the wilderness have survived, so that those taken in 1881 from the unmanured plot (plot 3) of the adjacent Permanent Wheat Experiment had to be used to represent the initial condition of the wilderness. Plot 3 runs up to the edge of the stubbed part of the present wilderness. For comparison, samples from the plot given sulphate of ammonia alone (plot 10) were also analysed. The initial weights of soil and stones per hectare were taken as those found for the Permanent Wheat Experiment in 1881, and are the means for all plots except those given organic manures (see Table 3). Samples of top-soil were taken from the wilderness in 1895. As the corresponding records of the weights of soil, stones, etc., could not be found, this sampling will not be considered further, other than to record the analyses done on a combined sample of the soil (Table 3). Two sampling holes were dug in 1904, one in the present stubbed section of the wilderness, and one on the edge of the present wooded part. In 1964 the stubbed and wooded parts were sampled separately: see Fig. 1 for sampling positions.

Geescroft. Because Geescroft wilderness is on the old experimental plots, it was possible to sample areas which had received fertiliser phosphorus in the past and other areas that had not. The 1883 (No P) samples were taken from plots 3 and 4 of the Continuous Beans Experiment: both plots received sodium nitrate alone. The 1883 (P) samples were from plots 6 and 7 (both receiving nitrogen and phosphorus) of the old beans experiment. Unfortunately the 9–18 inch (22·9–45·7 cm) sample from plots 6 and 7 has not survived and so a sample from this depth of plot 8, receiving nitrogen, phosphorus and potassium, was substituted. The only surviving figures for the weight of fine soil per hectare in 1883 came from plots on either side of the contemporary sampling lines: see Table 3. The precise position of the 1904 sampling holes is not known, but from the total phosphorus content of the sample, it must have come from the site of plots that had once received phosphorus (total phosphorus in the top 22·9 cm of plots 3 and 4 was 0·054%, in plots 6 and 7, 0·080% and in the 1904 samples 0·073%; Table 3). The 1964 and 1965 (No P) samples were taken on a line close to the division between plots 3 and 4; the 1964 (P) samples on a parallel line 12 m away, close to the old division between plots 6 and 7 (see Fig. 1).

Stand measurements. All tree stems with diameters exceeding 2·5 cm at a height of 1·3 m were counted and their girths measured on the central parts of both wildernesses in June 1969. In Broadbalk the area thus sampled (533 m²) was the whole site less the outer 5 m. In Geescroft the area sampled (4040 m²) was on plots 3–10 of the old beans

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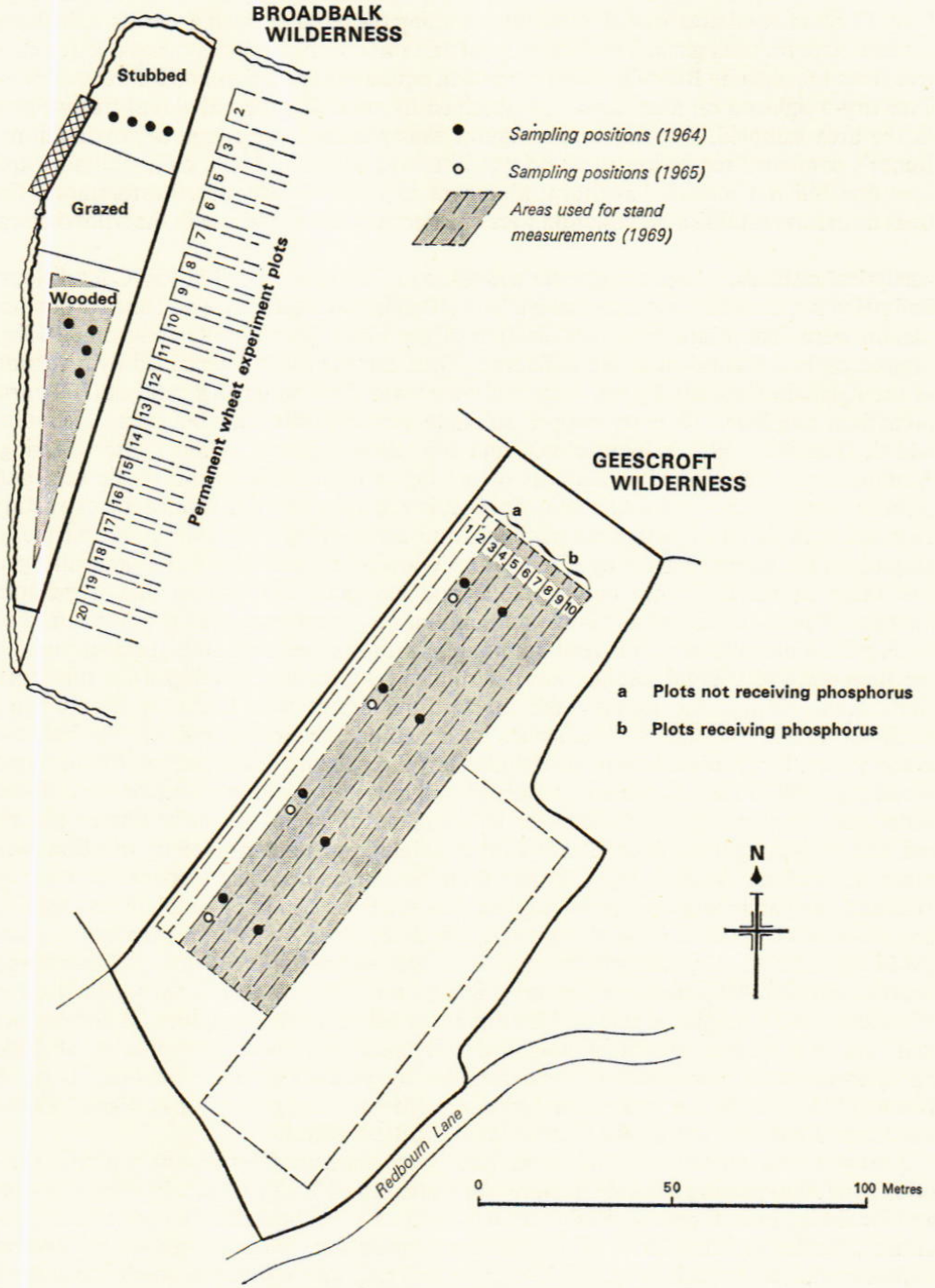

FIG. 1. Broadbalk and Geescroft wildernesses.

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experiment: all parts of the measured area were at least 8 m from the wilderness edge (Fig. 1). Stem basal area was obtained by summing the basal areas of the trees, calculated for each tree from its girth. Tree dry-weight (trunk and branches) was calculated for each tree from the girth by Bunce's (1968) regression equation for all sites and all tree varieties. Tree dry-weight on an area basis was obtained by summing the individual tree weights in the area sampled. The dry-weight figures thus obtained are rough approximations: Bunce's combined regression equation was obtained with ash, birch, oak, sycamore and lime and did not include hawthorn, abundant in both wildernesses. Furthermore, the trees he used to establish his equation were smaller than some of those in the wildernesses.

Analytical methods. Loss on ignition was estimated by igniting soil at 550°C for 1 hour. Soil pH was measured on a suspension of soil (10 g) in water (20 ml). Total and carbonate-carbon were determined by a modification of the Shaw procedure (Jenkinson, 1965b); organic carbon was taken as the difference. Total nitrogen was determined by a version of the Kjeldahl method; 2 g soil were moistened with 5 ml water, 2 g catalyst (100 parts potassium sulphate, 10 parts copper sulphate pentahydrate and 0·5 parts selenium) added, then 6 ml 98% sulphuric acid and the whole digested 2 hours after clearing. Ammonia was determined in aliquots of the digest by distillation into boric acid and titration with 0·005 N sulphuric acid. Inorganic nitrogen was determined by extracting 10 g soil with 50 ml N potassium sulphate, and determining ammonium and nitrate in aliquots of the filtered extract by d'Arifat and Warren's method (1964). Organic nitrogen was taken as the difference between total and inorganic nitrogen so that it includes nitrogen present in the soil as 'fixed' ammonium, i.e. ammonium nitrogen not extracted by N potassium sulphate: for fixed ammonium measurements on soils from Broadbalk see Bremner, 1959. Total sulphur was determined by a method developed for this work (Jenkinson, 1968b): the results were in close agreement with those by Bloomfield's method for total soil sulphur (1962) when both methods were compared on soils from the wildernesses. Inorganic sulphur was estimated by a procedure developed by Williams and Steinbergs (1962) for soluble and adsorbed sulphate: 10 g soil was shaken with 40 ml water and 1 g of calcium carbonate for 16 hours and the sulphate in the filtered extract reduced to hydrogen sulphide. The hydrogen sulphide was determined by titration with mercuric acetate (Archer, 1956) rather than by the colorimetric procedure used by Williams and Steinbergs. Organic sulphur was taken as total soil sulphur less soluble and adsorbed sulphate. Total phosphorus was determined by sodium carbonate fusion (Mattingly, 1970). Organic phosphorus was determined by Williams, Williams and Scott's method (1960), in which 2 g soil is ignited for 1 hour at 550°C, then extracted for 16 hours with 2N sulphuric acid and the difference between the phosphorus in this extract and that in a similar extract of unignited soil taken as organic phosphorus. Organic phosphorus was determined in some samples by another ignition method (Legg & Black, 1955) and by an extraction procedure (Mehta, Legg, Goring & Black, 1954). Mechanical analysis was by the international pipette method.

Nitrogen and carbon mineralisation rates were measured by incubating soil. Air-dried soil (50 g) passing a 0·635 cm sieve was wetted to 60% of its water holding capacity and incubated in a stoppered bottle for 10 days at 25°C in the dark. The bottle also contained a beaker holding 20 ml of N potassium hydroxide. Even though the incubation bottles contained enough oxygen (230 mg) for soil respiration over the whole incubation period, the bottles were aerated after six days. The amount of carbon dioxide absorbed in the alkali was calculated from the volume of standard hydrochloric acid required to bring the pH from 8·30 to 3·70, less that required by the blank. Nitrogen mineralisation

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was measured by determining nitrate and ammonium nitrogen in N potassium sulphate extracts of soil before and after incubation.

All analyses were done in duplicate and the analysis was repeated when discrepancies between duplicate results exceeded those usual with the measurement.

Sampling errors. Most analyses were done on bulked samples, made, for each soil layer, by combining equal weights of 30 mesh soil from each of the holes dug in a given site. To check the validity of this procedure, and also to estimate the significance of differences between sites, soil samples from each depth of the four holes dug per site in 1964 and 1965 were analysed separately, in duplicate, for total nitrogen. Total nitrogen was chosen as giving, in a single determination, a good measure of the organic matter in a soil.

Errors from sample bulking. Table 2 shows the nitrogen in oven-dry fine soil as found on the bulked sample (column C) and as the mean of four separate determinations on the individual samples (column B). Agreement was close: percentage nitrogen as found by the two procedures never differed by more than 0·005. Table 2 also shows

TABLE 2

Nitrogen in wilderness soils

Site	Sampling date	Sampling depth, cm	Oven-dry fine soil Mkg ha^{-1}	% N in oven-dry fine soil		N in oven-dry fine soil, kg ha^{-1}	
			A	B	C	D	E
Broadbalk wilderness, stubbed part	November 1964	0–22·9	2·32	0·266	0·261	6170	6060
		22·9–45·7	2·71	0·100	0·098	2700	2660
		45·7–68·6	3·09	0·074	0·075	2270	2320
Broadbalk wilderness, wooded part	November 1964	0–22·9	2·29	0·252	0·255	5750	5840
		22·9–45·7	2·71	0·099	0·099	2680	2670
		45·7–68·6	3·01	0·080	0·079	2400	2370
Geescroft wilderness, wooded	April 1965	0–22·9	2·19	0·166	0·168	3630	3670
		22·9–45·7	2·94	0·092	0·093	2720	2730
		45·7–68·6	3·12	0·067	0·072	2090	2230
L.S.D. ($P = 0·05$) between sites (9 D.F.)			0·22	0·015	—	490	—
L.S.D. ($P = 0·05$) between depths (18 D.F.)			0·17	0·012	—	400	—

A. Means of four measurements per site.
B. Samples from each hole analysed separately in duplicate: figures in this column are means of four such measurements per site.
C. Means of duplicate analyses on composite sample from all four holes.
D. Weights of nitrogen per hectare calculated individually for each hole from measurements made on that hole alone: figures in this column are means of four such measurements per site.
E. Mean weight of fine soil per hectare × per cent nitrogen in composite sample ÷ 100.

(column E) the weight of nitrogen in a given layer calculated from the weight of fine soil per hectare (mean of results from four holes) and the nitrogen content of the bulked sample. The weights of nitrogen per hectare given in column D are the means of four independent measurements, one from each hole, calculated from measurements made and analyses done on soil from that hole alone. The differences between columns D and E are small relative to the total amount of nitrogen in the soils, so that the errors introduced by sample bulking are relatively unimportant.

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Significance of differences between sites. Table 2 shows that the weights of fine soil per hectare in the top layer (0–22·9 cm) of Geescroft wilderness, the stubbed part of Broadbalk and the wooded part of Broadbalk do not differ significantly ($P = 0{\cdot}05$). In all three sites there was significantly less fine soil in the top than in the second layer, and significantly less in the second than in the third. The top layer of Geescroft contains significantly less nitrogen per hectare than the equivalent layer in either part of Broadbalk wilderness. There is less nitrogen in the top layer of the wooded part of Broadbalk than in the stubbed part, but the difference does not quite reach significance (Table 2, column D). The amounts of nitrogen in the second and third layers do not differ significantly between sites.

The accuracy of the sampling in 1881, 1883 and 1904 cannot now be assessed. Probably the sampling error was less in 1881 and 1883 than in 1964 and 1965 because more samples

TABLE 3

Sampling and analysis of soils

Site	Sampling date	Land use	Sampling depth,[1] cm	Oven-dry fine soil[2] Mkg ha^{-1}	Oven-dry stones Mkg ha^{-1}	Oven-dry roots Mkg ha^{-1}	Equivalent soil depths at different sampling dates,[3] cm
Broadbalk field	October 1881	Arable	0–22·9	2·87[9]	0·61[9]	—	22·9
			22·9–45·7	3·04[9]	0·38[9]	—	45·7
			45·7–68·6	3·10[9]	0·22[9]	—	68·6
,, ,,	October 1881	Arable	0–22·9	2·87[9]	0·61[9]	—	22·9
			22·9–45·7	3·04[9]	0·38[9]	—	45·7
			45·7–68·6	3·10[9]	0·22[9]	—	68·6
,, ,,	October 1895	Scrub	0–22·9	—	—	—	—
,, ,,	March 1904	Scrub	0–22·9	2·77[12,22]	0·51[12,21]	—	24·0
			22·9–45·7	3·01[12,22]	0·04[12,21]	—	47·4
			45·7–68·6	3·05[13,22]	0·03[12,21]	—	71·0
,, ,,	November 1964	Stubbed	0–22·9	2·32[11]	0·50[11]	0·006[11]	28·8
			22·9–45·7	2·71[11]	0·50[11]	0[11]	53·5
			45·7–68·6	3·09[11]	0·12[11]	0[11]	76·5
,,	November 1964	Wooded	0–22·9	2·29[11]	0·42[11]	0·022[11]	29·0
			22·9–45·7	2·71[11]	0·32[11]	0·014[11]	53·6
			45·7–68·6	3·01[11]	0·17[11]	0·005[11]	76·6
Geescroft field	April 1883	Arable (No P)	0–22·9	2·73[10]	—	—	22·9
			22·9–45·7	3·01[10,23]	—	—	45·7
			45·7–68·6	3·10[10,24]	—	—	68·6
,,	April 1883	Arable (P)	0–22·9	2·73[10]	—	—	22·9
			22·9–45·7	3·01[10,23]	—	—	45·7
			45·7–68·6	3·10[10,24]	—	—	68·6
,, ,,	April 1904	Scrub	0–22·9	2·71[12,22]	0·64[12,21]	—	23·1
			22·9–45·7	3·03[12,22]	0·35[12,21]	—	45·7
			45·7–68·6	3·13[13,22]	0·03[12,21]	—	68·1
,, ,,	April 1965	Wooded (No P)	0–22·9	2·19[11]	0·70[11]	0·007[11]	27·8
			22·9–45·7	2·94[11]	0·43[11]	0·003[11]	50·8
			45·7–68·6	3·12[11]	0·16[11]	0·002[11]	73·9
,, ,,	November 1964	Wooded (No P)	0–22·9	2·25[11]	0·73[11]	0·009[11]	—
,, ,,	November 1964	Wooded (P)	0–22·9	2·28[11]	0·76[11]	0·008[11]	—

[1] Sampling depths 0–9 inches, 9–18 inches and 18–27 inches in all cases.
[2] One Mkg ha^{-1} = 892 200 lb per acre.
[3] Depth to which soil must be sampled to contain the same weight of ignited fine soil per hectare as in the 0–22·9, 0–45·7 and 0–68·6 cm layers of Broadbalk in 1881 or of Geescroft in 1883.
[4] All from Broadbalk plot 3 (continuous wheat: unmanured).
[5] Six from Broadbalk plot 10A: six from 10B (both under continuous wheat and receiving N fertiliser alone).
[6] Two from Geescroft plot 3: two from plot 4 (both under continuous beans and receiving N fertiliser alone).
[7] Two from Geescroft plot 6: two from plot 7 (both under continuous beans and receiving N and P fertilisers).
[8] All from Geescroft plot 8 (continuous beans, receiving N, P, K, Na and Mg fertilisers).
[9] Mean of 108 measurements (six on each plot of the experiment, plots 2 and 19 excluded).
[10] Mean of 12 measurements (two on each of plots 1, 2, 9 and 10; four on plot 8).
[11] Mean of four measurements.
[12] Mean of two measurements.
[13] One measurement.
[14] Corrected for chalk removed from sample prior to sieving (0·53 g per 100 g oven-dry 0·635 cm sieve fine soil).
[15] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 2·64 g stones retained by a 0·3 cm sieve, plus 0·53 g chalk removed prior to sieving.

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were taken per site and the sites were then probably more uniform. Sampling errors were probably greater in 1904 than in preceding or subsequent samplings.

Results

Soil expansion during reversion to wilderness. Table 3 gives the weights of fine soil, stones and roots per hectare for the different sites and sampling dates. The soil has expanded: for example in 1881, the top layer (0–22·9 cm) of Broadbalk contained 2·75 million kg of ignited fine soil per hectare, whereas in 1964 the corresponding value for the stubbed section of the wilderness was only 2·15 million kg. For this example, the equivalent depth is defined as the depth to which the soil should have been sampled in 1964 to contain the same weight of ignited fine soil per hectare as when sampled to

TABLE 3 (*continued*)

Number of samples combined for analysis	Soil pH	As percentage oven-dry fine soil passing 0·635 cm sieve								
		Loss on ignition	Organic C	Carbonate C	Organic N	Inorganic N	Organic S	Inorganic S	Organic P	Inorganic P
6[4]	8·1	4·19	0·92	0·52	0·102	0·0024	0·0166	0·0015	0·0252	0·0408
6[4]	7·7	4·98	0·59	0·01	0·077	0·0010	0·0107	0·0017	0·0244	0·0255
6[4]	7·4	5·36	0·46	0	0·066	0·0004	0·0063	0·0013	0·0205	0·0216
12[5]	7·9	4·12	1·04	0·41	0·113	0·0022	0·0181	0·0020	0·0264	0·0378
12[5]	7·7	4·90	0·59	0·01	0·079	0·0013	0·0107	0·0021	0·0252	0·0270
12[5]	7·6	6·16	0·49	0·01	0·065	0·0008	0·0085	0·0017	0·0223	0·0257
7[25]	7·9	5·68	1·43	0·56	0·143	0·0026	0·0216	0·0014	0·0276	0·0385
2[15]	8·0	5·31[14]	1·34	0·46[14]	0·142	0·0006	0·0197	0·0015	0·0291	0·0351
2[16]	7·6	6·33	0·66	0·01	0·097	0·0012	0·0132	0·0017	0·0280	0·0305
2[17]	7·4	6·83	0·52	0·01	0·080	0·0010	0·0073	0·0013	0·0261	0·0284
4	7·8	7·48	2·79	0·29	0·260	0·0010	0·0397	0·0022	0·0420	0·0354
4	7·9	6·15	0·81	0·04	0·098	0·0001	0·0142	0·0015	0·0311	0·0273
4	7·7	6·71	0·55	0·01	0·075	0·0004	0·0091	0·0017	0·0287	0·0247
4	7·9	7·19	2·70	0·39	0·254	0·0009	0·0396	0·0021	0·0410	0·0416
4	8·0	4·67	0·85	0·16	0·098	0·0004	0·0162	0·0020	0·0309	0·0308
4	7·8	5·78	0·61	0·01	0·078	0·0004	0·0132	0·0020	0·0300	0·0303
4[6]	7·1	4·06	1·04	0	0·115	0·0025	0·0147	0·0012	0·0250	0·0292
4[6]	7·1	5·37	0·58	0	0·083	0·0008	0·0098	0·0011	0·0248	0·0272
4[6]	7·1	5·82	0·49	0	0·070	0·0011	0·0075	0·0011	0·0212	0·0268
4[7]	7·0	4·27	1·10	0	0·117	0·0024	0·0151	0·0014	0·0254	0·0547
4[8]	7·1	5·33	0·56	0	0·079	0·0015	0·0090	0·0014	0·0234	9·0224
4[7]	7·1	6·02	0·47	0	0·066	0·0007	0·0078	0·0013	0·0222	0·0217
2[18]	6·1	4·58	1·37	0	0·131	0·0023	0·0190	0·0015	0·0286	0·0445
2[19]	6·9	4·40	0·58	0	0·082	0·0010	0·0103	0·0012	0·0248	0·0283
2[20]	7·1	5·34	0·42	0	0·069	0·0004	0·0078	0·0011	0·0198	0·0266
4	4·5	5·93	1·98	0	0·166	0·0022	0·0267	0·0059	0·0327	0·0234
4	5·5	6·32	0·76	0	0·092	0·0008	0·0172	0·0062	0·0249	0·0256
4	6·2	6·52	0·49	0	0·071	0·0007	0·0117	0·0065	0·0204	0·0287
4	4·6	5·31	1·85	0	0·159	0·0017	0·0246	0·0050	0·0321	0·0236
4	4·7	5·21	1·82	0	0·156	0·0018	0·0236	0·0044	0·0344	0·0433

[16] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 2·24 g stones retained by a 0·3 cm sieve.
[17] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 1·43 g stones retained by a 0·3 cm sieve.
[18] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 2·53 g stones retained by a 0·3 cm sieve.
[19] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 1·39 g stones retained by a 0·3 cm sieve.
[20] Analytical results converted to 0·635 cm sieve basis by assuming that 100 g oven-dry fine soil (0·635 cm sieve) contains 1·20 g stones retained by a 0·3 cm sieve.
[21] Stones passing 0·635 cm sieve but retained by 0·3 cm sieve deducted.
[22] Stones passing 0·635 cm sieve but retained by 0·3 cm sieve added.
[23] Assuming 96·2% oven-dry fine soil in air-dried fine soil
[24] Assuming 94·7% oven-dry fine soil in air-dried fine soil } See Hall (1917), Chapter III, Table 12.
[25] Samples taken with a sampling box 12 inches square by 9 inches deep: Samples labelled 'Broadbalk Upper Butts'.

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22·9 cm in 1881. Equivalent depths were obtained graphically by plotting the weights of ignited fine soil per hectare in the 0–22·9, 0–45·7 and 0–68·6 cm layers against depth for each sampling date and then reading off the required figures, by extrapolation where necessary. Table 3 gives, for the different sampling dates, the equivalent depths for the 22·9, 45·7 and 68·6 cm sampling depths in 1881 (Broadbalk) or in 1883 (Geescroft).

For the top layer of Broadbalk, the equivalent depths were 22·9 cm (1881) and 28·8 cm (1964: stubbed); for all three layers, 68·6 cm (1881) and 76·5 cm (1964: stubbed). Thus most of the expansion occurred in the top layer. Soil expansion was less in Geescroft than in either part of Broadbalk wilderness.

These calculations of soil expansion assume that nothing leaving a residue on ignition has been added or lost from the various soil layers during the development of the wilderness. This assumption is probably not far wrong. The removal of calcium carbonate by leaching is almost certainly the biggest single loss: if all the chalk in the top 68·6 cm of Broadbalk in 1881 had been leached out by 1964, the equivalent sampling depth given in Table 3 (76·5 cm, stubbed section) would have been too large by only 0·6 cm.

A better basis for these calculations would probably have been the weights of ignited fine soil *plus* stones per hectare. However, because the weight of stones per hectare for Geescroft in 1883 is not known, it was decided to make all calculations on the basis of ignited fine soil alone. The errors thus introduced are small. Broadbalk contained 9·77 million kg ignited fine soil plus stones per hectare in the top 68·6 cm in 1881: to obtain this weight of ignited fine soil plus stones in 1964 it would have been necessary to sample the stubbed section to a depth of 76·8 cm, compared to a depth of 76·5 cm calculated on the basis of ignited fine soil alone.

Calculation of the net accumulation of soil constituents allowing for soil expansion. Because the soil has expanded, the layers sampled and analysed in 1964 do not correspond exactly to those sampled in 1881. Allowance must therefore be made for soil expansion in calculating the net accumulation of a constituent on an area basis for a given layer. This was done, graphically, for each soil constituent, by plotting the amounts in the 0–22·9, 0–45·7 and 0–68·6 cm layers against depth for each sampling date. Using the 'equivalent depths' given in Table 3, the amount of the soil constituent per hectare in a given soil layer at a given sampling was then read off. Table 4 gives the amounts of carbon (organic), nitrogen (organic), sulphur (total and organic) and phosphorus (total and organic) in equivalent layers of the two wildernesses at different sampling dates. These corrections for soil expansion are substantial: for example the top layer (0–22·9 cm) of Broadbalk wilderness (stubbed) *as sampled* in 1964 contained 3100 kg per hectare more organic nitrogen in 1964 than in 1881, whereas *when allowance is made for soil expansion*, the top 22·9 cm of soil in 1881 gained 3900 kg per hectare by 1964.

Table 5 shows the gains in organic carbon, organic nitrogen, organic sulphur and organic phosphorus in the top layer (0–22·9 cm) during reversion to wilderness. A similar table can be constructed for the whole profile from the results in Table 4. However, the errors in gains thus calculated for the whole profile are much greater than in the gains for the top layer: extrapolation to a depth greater than that sampled is necessary to correct for soil expansion in the whole profile, the lower layers are more heterogeneous than the top layer, and the whole-profile gains (especially of sulphur and phosphorus) are much smaller relative to the amounts originally present than are the gains in the top layer.

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TABLE 4

Carbon, nitrogen, sulphur, and phosphorus in equivalent soil layers

Site	Sampling date	Land use	Soil layer,[a] cm	Soil constituent,[b] kg ha^{-1}					
				Organic C	Organic N	Total S	Organic S	Total P	Organic P
Broadbalk field	October 1881	Arable[e]	0–22·9[e]	26 300	2930	520	480	1890	720
			0–68·6[f]	58 000	7300	1130	1000	4710	2100
	October 1881	Arable[d]	0–22·9[e]	29 700	3240	580	520	1840	760
			0–68·6[f]	63 000	7600	1280	1110	4910	2210
	March 1904	Scrub	0–24·0[e]	38 600	4110	620	570	1860	850
			0–71·0[f]	73 000	9600	1320	1190	5360	2520
	November 1964	Stubbed	0–28·8[e]	71 800	6860	1100	1040	2230	1200
			0–76·5[f]	109 000	11 800	1840	1670	5650	3020
	November 1964	Wooded	0–29·0[e]	69 400	6600	1110	1040	2380	1170
			0–76·6[f]	110 000	11 600	2060	1880	6000	2990
Geescroft field	April 1883	Arable (No P)	0–22·9[g]	28 400	3150	430	400	1480	680
			0–68·6[h]	61 000	7800	1030	930	4540	2080
	April 1883	Arable (P)	0–22·9[g]	30 000	3210	450	410	2190	690
			0–68·6[h]	61 000	7600	1050	930	4930	2080
	April 1904	Scrub (P)	0–23·1[g]	37 400	3610	560	520	2020	780
			0–68·1[h]	68 000	8100	1180	1070	5010	2130
	April 1965	Wooded (No P)	0–27·8[g]	49 300	4240	860	700	1550	870
			0–73·9[h]	84 000	9000	2100	1530	4610	2210

[a] Equivalent layers (see Table 3) have same suffix, i.e. [e], [f], [g], or [h].
[b] 1 kg ha^{-1} = 0·8922 lb per acre.
[c] Plot 3; see Table 3.
[d] Plot 10; see Table 3.

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TABLE 5

Organic carbon, nitrogen, sulphur and phosphorus gained by the top 22·9 cm (9 inches) of soil during reversion to wilderness

		Broadbalk stubbed	Broadbalk wooded	Geescroft wooded
Gained by soil since 1883,[a,b] kg ha^{-1}	Organic C	45500	43100	20900
	Organic N	3930	3670	1090
	Organic S	560	560	300
	Organic P	480	450	190
Mean annual gain, kg ha^{-1} year^{-1}	Organic C	560	530	250
	Organic N	49	45	13
	Organic S	6·9	6·9	3·7
	Organic P	5·9	5·6	2·3
Initial soil ratios[b]	C/N	9·0	9·0	9·0
	S/N	0·16	0·16	0·13
	P/N	0·25	0·25	0·22
Ratios in gain	C/N	11·6	11·7	19·2
	S/N	0·14	0·15	0·28
	P/N	0·12	0·12	0·17

[a] All gains calculated on an equivalent depth basis.
[b] For Broadbalk the initial status is taken to be that of Broadbalk plot 3, as sampled in 1881: for Geescroft that of Geescroft plots 3 + 4, as sampled in 1883.

Changes in the wildernesses over the experimental period

pH. The calcium carbonate reserves of the Broadbalk wilderness site ensured that changes in pH between 1881 and 1964 were trivial. In contrast, Geescroft had no carbonate reserves, and the pH of the top layer (0–22·9 cm) fell from 7·1 in 1883 to 6·1 in 1904 and to 4·5 in 1965 (Table 3). Acidity increased less in the lower soil horizons.

Organic carbon. The wooded and stubbed parts of Broadbalk have accumulated almost exactly the same amounts of organic carbon during 81 years: more than 80% of the gain occurred in the top layer. The annual accumulation rate in Geescroft was only about half the rate in Broadbalk: again the accumulation was mainly in the top layer. Both wildernesses gained organic carbon slightly faster before than after 1904.

Organic nitrogen. As with carbon, the wooded and stubbed parts of Broadbalk have accumulated almost the same amount of organic nitrogen in 81 years, most of the accumulation also being in the top layer. The 1904 samples from the 45·7–68·6 cm layer contained more nitrogen than either of the corresponding 1964 samples (Table 3). Hall found the total nitrogen content of the 1904 sample to be 0·0839% (Hall, 1905); my result for the same sample was 0·0823% so that nitrogen gain during storage can be discounted. Organic carbon behaved differently: being less in the 1904 sample than in the 1964 samples, as would be expected. Because of this peculiarity in the nitrogen content of the 45·7–68·6 cm layer, and to a lesser extent, the 22·9–45·7 cm layer, the 1904 results for these layers have not been used in calculating annual accumulation rates etc.

The annual accumulation rate in the top layer of the stubbed site during the first 21 years was 56 kg organic nitrogen per hectare per year, slightly greater than during the succeeding 60 years (46 kg per hectare per year). Over the whole period the stubbed part of Broadbalk gained 49 kg per hectare per year in the top layer and 55 kg per hectare per year in the whole profile. The corresponding figures for the wooded part are 45 and 53 kg per hectare per year. Geescroft accumulated much less nitrogen: little more than

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quarter of that gained by Broadbalk. Here the annual accumulation of organic nitrogen in the top layer was 13 kg per hectare per year; in the whole profile, 15 kg per hectare per year.

Relative to their organic nitrogen contents, the inorganic nitrogen contents of all the soils are small (see Table 3), so that gains in organic nitrogen can be taken as gains in total nitrogen without introducing errors of more than 1–2%.

Sulphur. The top layers of the wooded and stubbed section of Broadbalk wilderness gained about the same amount of organic sulphur in 81 years. However, the two lower layers of the wooded part contained 840 kg organic sulphur per hectare in 1964, compared with 640 kg in the corresponding layers of the stubbed part. No completely satisfactory explanation of this difference between sites can be given. It is unlikely to be due to analytical error: the total sulphur contents of the 1964 Broadbalk samples were determined by X-ray fluorescence spectrometry and the values obtained were all within 10 ppm of those given in Table 3 (Brown & Kanaris-Sotiriou, personal communication). If subsoil heterogeneity is the explanation, then the additional organic sulphur might be expected to be accompanied by additional organic carbon. The 22·9–45·7 and 45·7–68·6 cm layers of the wooded part do contain more carbon than the corresponding layers in the stubbed part, but the differences are less than those for organic sulphur (Table 3).

Calcareous soils can contain water-insoluble sulphate associated with the calcium carbonate (Williams, Williams & Scott, 1960). Such sulphur would be reported as 'organic' in Tables 3, 4 and 5. However, it is improbable that the Broadbalk soils contain much such 'organic' sulphur because the chalk in them contains little sulphur. Chalk hand-picked from the top layer (0–22·9 cm) of the stubbed section of Broadbalk wilderness contained only 190 ppm total sulphur.

The mean annual gain for the top layer of Geescroft was 3·7 kg organic sulphur per hectare per year, roughly half the corresponding gain for Broadbalk (6·9 kg organic sulphur per hectare per year). Inorganic sulphur behaved differently: the mean annual gain for the top layer of Geescroft was 1·6 kg inorganic sulphur per hectare per year, but in Broadbalk the gain was negligible (0·2 kg inorganic sulphur per hectare per year).

Phosphorus. The total phosphorus content of the whole profile of Broadbalk was 4710 kg per hectare in 1881, 5360 kg per hectare in 1904, 5650 kg per hectare in the stubbed part of the wilderness in 1964 and 6000 kg per hectare in the wooded part in 1964, all on an equivalent depth basis. This gain may not be real, because the 1881 samples from plot 3, taken to represent the status of the soil before the wilderness was allowed to develop, may have contained less phosphorus than the actual wilderness site, especially that part of it now wooded. It is also possible that phosphorus could have been brought up from below 68·6 cm by deep rooting plants, although this is unlikely as the gain in phosphorus between 1881 and 1964 is much less in the top layer (0–22·9 cm) than in the 22·9–68·6 cm layer (Table 4). Phosphorus brought up from the deep subsoil would almost certainly accumulate mainly in the top layer, the layer that receives most of the incoming plant debris. Chance contamination by phosphorus-containing materials cannot be completely excluded as the site is so near the present farm buildings, but is unlikely in a carefully preserved experimental area.

In Geescroft, the initial samples came from the area that is now wooded, and the total phosphorus content of the 1965 samples corresponds closely with that of the 1883 (No P) samples (Table 4). In 1964, parts of the wilderness that had once received superphosphate

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TABLE 6

Organic phosphorus in soil, as determined by different methods

Soil		Broadbalk plot 3, sampled 1881 0–22·9 cm	Broadbalk plot 3, sampled 1881 45·7–68·6 cm	Broadbalk stubbed, sampled 1964 0–22·9 cm	Broadbalk stubbed, sampled 1964 45·7–68·6 cm	Geescroft wooded, sampled 1965 0–22·9 cm	Geescroft wooded, sampled 1965 45·7–68·6 cm
		ppm P in oven-dry soil					
Total		660	421	774	534	561	491
Method A	Extracted from untreated soil	188	79	195	59	126	65
	Extracted from ignited soil	440	284	615	346	452	268
	Organic	252	205	420	287	326	203
Method B	Extracted from untreated soil	207	84				
	Extracted from ignited soil	442	286				
	Organic	235	202				
Method C	Extracted from untreated soil	305	239	326	287	250	253
	Extracted from ignited soil	482	312	591	369	455	322
	Organic	177	73	265	82	205	69
Method D	Extracted from untreated soil	305	239				
	Extracted from ignited soil	486	319				
	Organic	181	80				
Method E	Total P extracted	473	316	590	379	460	341
	Inorganic P extracted	327	278	391	372	301	310
	Organic	146	38	199	7	159	31

Method A—Extract 2 g soil 16 hours with 100 ml 2N H_2SO_4. Ignite at 550°C for 1 hour.
Method B—Extract 0·5 g soil 16 hours with 100 ml N H_2SO_4. Ignite at 550°C for 0·5 hours.
Method C—Extract soil with concentrated HCl. Ignite at 240°C for 1 hour.
Method D—Ignite at 550°C for 1 hour. Otherwise as C.
Method E—Extract soil with concentrated HCl, then with 0·5N NaOH.

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and parts that had not were sampled separately. Table 3 shows that the additional phosphorus made no difference to the amounts or organic carbon, nitrogen or sulphur accumulating in the top 22·9 cm of soil.

The division of soil phosphorus into organic and inorganic parts in Tables 3 and 4 is suspect. The organic phosphorus values in these Tables were measured by Williams, Williams and Scott's (1960) method, hereafter called method A. Organic phosphorus measurements by method A were compared with those by four other methods on six of the soils appearing in Table 3. Table 6 shows that there is poor agreement between the different methods, especially when applied to subsoils. Method A, in which organic phosphorus is taken as the difference between the phosphorus soluble in cold 2N sulphuric acid before and after ignition, always gave the largest value. Method B is a slight modification of method A, using N sulphuric acid as extractant: it gives substantially the same results as method A. In method C, organic phosphorus is taken as the difference between the phosphorus soluble in hot concentrated hydrochloric acid before and after ignition. Slightly more phosphorus is dissolved after ignition than in method A, but as much more inorganic phosphorus is dissolved from the unignited soil, method C gives considerably smaller values for organic phosphorus than method A. The differences between the amounts of phosphorus extracted by hot concentrated hydrochloric acid and cold 2N sulphuric acid from the unignited soils are 131 and 228 ppm for the 1964 Broadbalk topsoil and subsoil respectively; as the subsoil contains much less organic matter, these differences are unlikely to represent organic phosphorus hydrolysed by hot hydrochloric acid but not by cold dilute 2N sulphuric acid. A more plausible explanation of the discrepancy between methods A and B is that a fraction of originally insoluble *inorganic* phosphorus is rendered soluble in cold 2N sulphuric acid by ignition, whereas this fraction is soluble in hot concentrated hydrochloric acid whether or not the soil has been ignited: with method A this fraction would be reported as organic phosphorus. Method D is the same as method C except that the soil is ignited at 550°C instead of at 240°C: the two methods give almost the same results. In method E the soil is extracted with hot concentrated hydrochloric acid, followed by cold and hot 0·5N sodium hydroxide: the difference between total and inorganic phosphorus in the combined extracts is called organic phosphorus. Values obtained by this method were smaller and more variable than by the other four methods. The total amount of phosphorus extracted did not differ greatly from that extracted from ignited soil by hot concentrated hydrochloric acid (method C), suggesting that extraction was complete, and that this method gives low values for organic phosphorus because organic phosphorus is hydrolysed during extraction.

Methods A, C and E all show that organic phosphorus in the top 22·9 cm of the Broadbalk soil increased as the stubbed site reverted to wilderness. In 81 years the amounts of organic carbon, nitrogen and sulphur in the top layer of soil from this site all more than doubled, whereas the increase in organic phosphorus by method A was 67%, by method C, 50% and by method E, 36%. Thus, despite the discrepancies, all three methods indicate that the gain of organic phosphorus, relative to the initial content, is much less than that of organic nitrogen, organic carbon or organic sulphur (Table 3). Little else can be said about the organic phosphorus results in Tables 3, 4, 5 and 6 until more is known about the measurement of organic phosphorus in soil.

Mineralisation of nitrogen and carbon by soils from the wildernesses. Table 7 shows that the C/N ratio of the organic matter mineralising in Geescroft lies between the corresponding ratios for the wooded and stubbed parts of Broadbalk. Ammonium is nitrified almost

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TABLE 7

Mineralisation of carbon and nitrogen by soils from the wildernesses

Soil[a]	Broadbalk stubbed, sampled 1964	Broadbalk wooded, sampled 1964	Geescroft wooded, sampled 1964	Geescroft wooded, sampled 1965
ppm NO_3-N initially in soil	1	3	12	13
ppm NH_4-N initially in soil	8	8	7	7
ppm NO_3-N in soil after incubation	71	83	13	15
ppm NH_4-N in soil after incubation	4	4	28	32
ppm N mineralized during incubation	66	76	22	27
ppm CO_2-C mineralised during incubation	650	490	190	210
C mineralised during incubation / N mineralised during incubation	9·9	6·5	8·6	7·8
organic C initially in soil / organic N initially in soil	10·7	10·6	11·6	11·9

[a] 0–22·9 cm sample (see Table 3) in all cases.

TABLE 8

Stand measurements in Geescroft and Broadbalk wildernesses

Species	No. stems per ha[a]	Stem basal area,[b] $m^2\ ha^{-1}$	Dry weight $kg\ ha^{-1}$
GEESCROFT			
Hawthorn (*Craetagus monogyna*)	300	3·6	14500
Oak (*Quercus robur*)	167	16·5	105100
Elm (*Ulmus* spp.)	155	2·0	8400
Ash (*Fraxinus excelsior*)	140	8·5	46700
Elder (*Sambucus nigra*)	118	0·4	1100
Maple (*Acer campestre*)	29	0·4	1500
Sycamore (*Acer pseudoplatanus*)	2	0·3	1600
Hazel (*Corylus avellana*)	2	0·02	50
Silver birch (*Betula pendula*)	2	0·2	1400
All species	915	31·9	180000
BROADBALK			
Hawthorn (*Craetagus monogyna*)	1801	22·0	88600
Sycamore (*Acer pseudoplatanus*)	394	9·1	50300
Hazel (*Corylus avellana*)	281	1·9	6100
Ash (*Fraxinus excelsior*)	206	17·4	104100
Maple (*Acer campestre*)	38	3·6	21500
Elder (*Sambucus nigra*)	19	0·04	110
Oak (*Quercus robur*)	19	0·8	3600
All species	2758	54·8	274000

[a] With stem diameter >2·5 cm at a height of 1·3 m.
[b] At a height of 1·3 m.

completely in the Broadbalk soils during incubation; in the Geescroft soils little, if any, nitrification occurs during incubation, although the soil initially contained some nitrate. This is almost certainly because the pH of the Geescroft soils is near the lower limit for nitrification (Weber & Gainey, 1962).

Stand measurements on the trees in Broadbalk and Geescroft wildernesses. Table 8 gives the number of tree stems, stem basal area and calculated dry-weight of trunks and canopy for the wildernesses, all per hectare. All three values are greater on Broadbalk

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than on Geescroft, suggesting that annual production is greater in Broadbalk, although differences in the botanical colonisation sequence (Hall, 1905; Brenchley & Adam, 1915; Thurston, 1958) could also contribute to the present difference in tree dry-weight between the two sites.

Discussion

Accumulation of organic carbon by the wilderness soils. Organic matter accumulates in soil at a rate depending on the annual input of plant material and on the rate at which this plant material decomposes. Thus the smaller rate of accumulation in Geescroft could be caused by a smaller annual input or a greater annual loss than in Broadbalk, or by a combination of both. Stem basal area and calculated dry weight of trunks and canopy (Table 8) are both greater on the wooded part of Broadbalk than on Geescroft and there can be little doubt that more organic matter enters the soil each year in Broadbalk than in Geescroft. There is much more under-story vegetation on Broadbalk than on Geescroft, further increasing the productivity difference between the sites.

First consider factors that could cause the production of plant material (and hence the amount of organic matter entering the soil) to be less on Geescroft than on Broadbalk. External climatic factors such as sunlight, rainfall, and temperature cannot be involved as these are substantially the same for two adjacent sites of similar topography and altitude. Although stand measurements were done on the central parts of the wildernesses to minimise edge effects, the wooded part of Broadbalk is so much smaller (0·13 ha) than the wooded part of Geescroft (1·3 ha) that some of the productivity difference between the sites (Table 8) may result from the greater importance of edge effects on Broadbalk. For example, more light probably reaches the centre of the wilderness from the edge in Broadbalk than in Geescroft.

Brenchley and Adam (1915) considered that the botanical differences between the two sites indicated Geescroft to be the wetter, and forecast that Geescroft was too wet to revert to woodland. The appearance of the profiles shows that drainage is, or has been, more impeded on Geescroft than on Broadbalk (Appendix). However, this drainage difference cannot be great because the mechanical composition of the two sites is almost identical, both are tile-drained, and both have slight slopes. Drainage has not been sufficiently impaired on Geescroft to prevent reversion to woodland. Differences in drainage and structure between Geescroft and Broadbalk did not restrict plant production on Geescroft in the pre-wilderness period; plot 7 on Broadbalk (receiving nitrogen, phosphorus, potassium and magnesium) produced 2100 kg of wheat per hectare per annum over the period 1869–73, whereas plot 14 on Geescroft, given the same manurial treatment, gave 2400 kg oats per hectare, both good yields by the standards of that time. It is most improbable that the drainage of the two sites differs enough to account for the difference in productivity.

Differences in pH are unlikely to have influenced plant production directly, at least over the first few decades. By 1904 the pH of the Geescroft topsoil had only fallen to 6·1, yet the accumulation of organic carbon was markedly less than on Broadbalk.

Differences in productivity caused by potassium and phosphorus can be excluded. Both sites contain about the same amount of exchangeable potassium: the top layer of the 1904 Geescroft soil contained 116 ppm exchangeable potassium and the corresponding Broadbalk sample 117 ppm. Were plant production limited by phosphorus deficiency in Geescroft, then the part that used to receive phosphate should have produced more plant material than the part that had never received any. This difference

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should then have been reflected in the amount of organic matter entering the soil and hence on the amount of organic carbon accumulated by the soil. No such difference was found, so that Geescroft is not a site of the type discussed by Walker and Adams (1958), where organic production is limited by soil phosphorus.

The most probable reason for Geescroft producing less organic matter than Broadbalk is that less nitrogen is available for plant growth. Soil from Broadbalk now mineralises more than twice as much nitrogen as soil from Geescroft (Table 7). This difference has developed because the capacity of the two sites to accumulate nitrogen differs: see next section.

The other factor influencing the accumulation of organic matter in a soil is the rate at which the incoming organic matter decomposes. As the pH difference between Geescroft and Broadbalk widened, the rates of decomposition on the two sites may also have diverged. Experiments on the decomposition of carbon-14 labelled ryegrass in Rothamsted soils, of similar clay content but different pH, showed that, although decomposition was slower in acid soils at first (Jenkinson, 1965a), by the end of five years the difference between acid and calcareous soils had almost disappeared (Jenkinson, 1968a). Kononova (1966; p. 252) suggested that humic materials are more stable under calcareous than under non-calcareous conditions. If this is so, the decomposition curves for the carbon-14 experiments will cross over and less labelled carbon will remain in acid soils, after (say) 100 years, than in the corresponding calcareous ones. Broadbalk would then accumulate soil organic matter faster than Geescroft because it receives more plant material each year *and* because organic matter is more stable under calcareous conditions. The relative importance of these two mechanisms cannot be assessed from the data in this paper.

Accumulation of nitrogen by the wildernesses

Site accumulation. The total site gain by the wooded parts of Broadbalk and Geescroft exceeds the soil gain by the amount of nitrogen in the standing vegetation. This was not measured but its order of magnitude can be established from Ovington's (1962) figures for the dry-weights and nitrogen contents of broad-leaved deciduous English forests. The mean nitrogen content of the above-ground part of the trees from nine different sites was 0·386%. Applying this figure to the tree weights for Broadbalk and Geescroft wildernesses (Table 8), the trunks and canopy on Broadbalk contained 1100 kg nitrogen per hectare, those on Geescroft 700 kg nitrogen per hectare. The nitrogen in the over-wintering vegetation on the stubbed part of Broadbalk is negligible, compared with the amount in the soil. Neglecting the understory nitrogen and the nitrogen in large roots, and taking the gain in soil organic nitrogen as the gain in total soil nitrogen, the total site gain for the wooded part of Broadbalk wilderness is then 65 kg per hectare per year (12 kg in the standing vegetation, plus 53 kg in the soil to a depth of 68·6 cm), comparable with recent results for woodlands from different parts of the world (Ovington, 1962; Richards, 1964; Moore, 1966). The stubbed part of Broadbalk gained a little less nitrogen (55 kg per hectare per annum) and Geescroft much less, 23 kg (8 kg in the standing vegetation plus 15 kg in the soil). Although these estimates of vegetation nitrogen are rough, most of the site gain is in the soil, so that errors of even 50% in the vegetation nitrogen estimate will not greatly influence the total site gain.

Sources of the nitrogen accumulating in the wildernesses

Rainfall. Over the period 1889–1903 the mean annual amount of mineral nitrogen carried down in the rain at Rothamsted was 4·4 kg per hectare, of which 1·3 kg per hectare

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was nitrate nitrogen, and 3·1 kg per hectare was ammonium nitrogen (Hall, 1917; Chapter II, Table 7). Over the period January 1960–December 1964 the corresponding total was 5·4 kg per hectare, of which 2·4 kg was nitrate nitrogen and 3·0 kg was ammonium nitrogen. These values, together with all the other values in this paper for the chemical composition of rain and air over the period January 1960–December 1964, are means of monthly samples analysed by the Government Chemist under the direction of the Meteorological Office: for the procedure used see Stevenson (1968).

'Dry' sorption of ammonia. The mean annual ammonia content of the air at Rothamsted over the period January 1960–December 1964 was 4·8 μg per m^3. Eriksson (1968), reviving earlier theories, suggested that the soil: plant system absorbs part of this atmospheric ammonia, and he constructed a map from the ammonia concentrations over Western Europe during 1958 in which the dry deposition of ammonia at Rothamsted was calculated to be 13 kg nitrogen per hectare per year.

The construction of the new farm buildings with their attendant manure heaps, cattle stalls etc., within 200 m of the Broadbalk wilderness will have provided a new source of ammonia (see Hutchinson & Viets, 1969). Some ammonia may reach the wilderness directly from the farm buildings but the amount is unlikely to be large because if it were, the crop on the adjacent unmanured plot 3 of the Permanent Wheat Experiment should also gain nitrogen by the same process. Johnston (1969a) showed that the wheat on plot 3 took up about the same amount of nitrogen annually in 1966–67 as in 1852–61, long before the new buildings were erected.

Organic nitrogen in dust, rain, bird droppings etc. Allen, Carlisle, White and Evans (1968) found, for four sites in England, that between 2·8 and 5·4 kg organic nitrogen per hectare per year was collected in their rain gauges, the largest amounts coming from the sites nearest heavy industry. Organic nitrogen in their rain gauges was from 28 to 50% of the inorganic nitrogen. These results make it improbable that more than 2 or 3 kg organic nitrogen per hectare per year are added to the soil at Rothamsted from this source. From analyses done almost 100 years ago, Miller (1905) put the Rothamsted figure at 1·5 kg per hectare per year. Birds will concentrate nitrogen in the wilderness by collecting food from the surrounding cultivated areas and defecating in the wooded parts of the wilderness. Although this may be important near roosting and nesting areas (Weir, 1969), it is unlikely to be important over whole sites: in any case the soil under the wooded part of Broadbalk, home to vast numbers of sparrows, contains no more nitrogen than the soil of the stubbed part.

Symbiotic fixation. Legumes once occurred on both parts of Broadbalk wilderness (Brenchley & Adam, 1915), but are now confined to the stubbed part, where *Lathyrus pratensis* is the only legume present (Thurston, personal communication). By 1913 legumes had disappeared from all but the margin of the wooded part (Brenchley & Adam, 1915). Geescroft grew a good crop of red clover in 1883, 1884 and 1885: Gilbert (1890) estimated, from soil and crop analyses, that roughly 170 kg nitrogen per hectare was fixed per year over this period, of which the soil gained about 60 kg per year. However, the clover soon died out in Geescroft and thereafter legumes comprised a very small part of the vegetation (Hall, 1905), although found in the botanical surveys of 1895, 1898, 1903 and 1913. None were present when the site was examined in 1957 (Thurston, personal communication). The reason for the early disappearance of legumes in Geescroft is unknown; even as late as 1913 the site contained open areas where they might have

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been expected. It follows that legumes have played a negligible role in fixing nitrogen in the wooded parts of both wildernesses, except possibly during the early years of Broadbalk.

No known nodulating non-legume able to fix nitrogen, for example alder (*Alnus incana*), has ever been recorded in either Broadbalk or Geescroft wilderness. Moore (1966) reviewed work suggesting that the roots of some non-nodulating plants can form associations with microorganisms that fix nitrogen. More evidence is needed before ascribing a significant role to such associations in the Rothamsted wildernesses.

Non-symbiotic fixation. Ashby (1907) found that soil from Broadbalk wilderness fixed more than twice as much nitrogen as soil from Geescroft wilderness when incubated with mannitol: *Azotobacter chroococcum* were 'abundant' in the Broadbalk samples but the Geescroft soil contained none. Ziemiecka (1932) found more *Azotobacter* in the stubbed than in the wooded sections of Broadbalk wilderness, but even the former contained far fewer than plot 3. In 1960 Burlingham (see Meiklejohn, 1969) failed to find *Azotobacter* in the stubbed part of Broadbalk wilderness. This evidence strongly suggests that *Azotobacter* now play a negligible role in the accumulation of nitrogen in the soils of these wildernesses.

Broadbalk soil contains *Clostridium pasteurianum* cells in larger numbers than *Azotobacter* (Meiklejohn, 1956). Soil from plot 3 incubated with straw under semi-anaerobic conditions fixed nitrogen vigorously (Barrow & Jenkinson, 1962) and it may be that anaerobes are the active fixing agents in Broadbalk wilderness. Some of the nitrogen accumulated by Geescroft may also have been fixed anaerobically, especially during the early years when the soil was less acid and organic matter accumulated faster.

Algae are sometimes plentiful enough in Broadbalk wheat field to form a crust on the surface soil (Bristol Roach, 1927). Dart and Roughley (personal communication) found that crusts from Broadbalk actively reduce acetylene to ethylene and so presumably fix nitrogen. Whether or not enough light reaches the soil surface in the wildernesses for significant fixation by blue-green algae is not known.

Nitrogen balance. The accumulation of nitrogen by a site depends on the annual input *and* on the extent to which the soil: plant system can retain nitrogen. Inorganic nitrogen alone cannot cause accumulation of organic matter: in 1966 the mean nitrogen content of the top 23 cm of plot 10 of the Permanent Wheat Experiment was 0·106%, little more than that of plot 3, although by then plot 10 had received 12 000 kg nitrogen per hectare as sulphate of ammonia during the 123 years of the experiment (Johnston, 1969b). When an old arable site reverts to wilderness, the amount of organic matter entering the soil each year increases, so that there is more substrate for heterotrophic nitrogen-fixation and also more plant carbon to stabilise nitrogen. In the Broadbalk wilderness the C/N ratio of the soil organic matter has changed little, suggesting that the ability of decomposing plant carbon to retain nitrogen has altered little during the development of these wildernesses. By contrast, in Geescroft the C/N ratio has steadily increased since the start (Table 5). This has not been caused by the lack of mineral nitrogen for microbial attack on accumulating plant residues of wide C/N ratio; the C/N ratio of the organic matter *mineralized* in Geescroft is not very different from the ratio of that mineralized by either the wooded or stubbed part of Broadbalk (Table 7).

Thus, although biological fixation of nitrogen is almost certainly less in Geescroft than in Broadbalk, this is not the only difference between the sites: the process by which decomposing plant carbon stabilises nitrogen in a residue with a C/N ratio of about 10 in calcareous Broadbalk is less effective in acid Geescroft.

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The large nitrogen gains in both parts of Broadbalk wilderness cannot be satisfactorily explained at present. Similar gains in wooded and stubbed parts point to mechanisms that are independent of vegetation type. The relatively small gain in Geescroft suggests that little of the nitrogen gained by the Broadbalk wildernesses can have come from rain, dust or atmospheric ammonia, which would have supplied equal amounts of nitrogen to all the sites. Most of the nitrogen fixed by the Broadbalk wildernesses must have been fixed biologically, but not, in the wooded part at least, by free-living azotobacter, by algae, or in symbiosis with legumes.

Accumulation of sulphur by the wildernesses. Sulphate sulphur accumulates in Geescroft but not in Broadbalk, presumably because positive sites, able to retain anions, developed in Geescroft as the pH fell.

There was more than enough sulphur in precipitation alone to account for all the sulphur gained by the wilderness soils. Miller (1905) found that Rothamsted rain deposited 7·8 kg of sulphur per hectare per year over the period 1881–87. Recent measurements are even larger: between January 1960 and December 1964 (inclusive) the rain deposited an average of 12·5 kg sulphur per hectare per year. Soils and plants can gain sulphur by direct absorption of atmospheric sulphur dioxide (Johansson, 1959; Spedding, 1969) and the amounts of sulphur entering the soil by this process probably greatly exceed the amounts carried down in the rain. Eriksson (1968) calculated that the 'dry' deposition of sulphur at Rothamsted was six times that carried down in precipitation in 1958. Thus sulphur accumulation in the wilderness soils has been limited not by supply but by the sulphur-retaining power of the soil.

Summary

The accumulation of soil organic carbon, nitrogen, sulphur and phosphorus was measured in three sites that had not been cultivated since 1883. The sites had previously been arable for centuries, and are located on the same soil series within 1·3 km of each other. Two had once been chalked and are still calcareous; in the third the pH, 7·1 in 1883, had fallen to 4·5 in 1965. The non-calcareous site, and one of the calcareous sites, have been undisturbed and are now deciduous woodland. Tree seedlings are regularly removed from the other calcareous site by stubbing.

Despite completely different vegetation, the soils of the calcareous stubbed and wooded sites have gained similar amounts of organic carbon, nitrogen, sulphur and phosphorus. In contrast, organic carbon, nitrogen, sulphur and phosphorus have all accumulated more slowly in the soil of the non-calcareous wooded site than in the soil of the calcareous wooded site. The wooded non-calcareous site gained 23 kg nitrogen per hectare per year over a period of 82 years (15 kg in the soil to a depth of 68·6 cm, plus an estimated 8 kg in the trees). The stubbed site gained 55 kg nitrogen per hectare per year over a period of 81 years (all in the soil), and the wooded calcareous site 65 kg over a period of 81 years (53 in the soil plus an estimated 12 kg in the trees). These differences between the sites are attributed to the increasing acidity of the non-calcareous soil. Little of the nitrogen gained by the two wooded sites can have been fixed in symbiosis with legumes, as legumes have long been absent from both.

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APPENDIX

Profile Descriptions of Wilderness Soils

B. W. AVERY and D. W. KING

The descriptions of colour, texture, structure and consistence are in accordance with the U.S.D.A. Soil Survey Manual, 1951. Horizon designations are after Avery (1964).

Geescroft wilderness (wooded)

L	2–0 cm	Litter layer (mainly current leaf fall).
A	0–4 cm	Very dark greyish brown (10 YR 3/2) slightly stony loam or silt loam; brown when crushed; stones mainly small angular flints and flint pebbles; moderate fine sub-angular blocky and granular structure; friable, soft; irregular penetration of organic matter with corresponding variations in colour and structure; worm casts present; abundant fine woody roots; sharp irregular boundary.
Eb	4–28 cm	Brown (10 YR 4/4–5/4) stony loam with common darker coloured channel fillings and ped coatings, especially in the upper part; few, fine, faint, paler coloured and ochreous mottles locally; stones as above; weak medium to coarse blocky structure; friable to firm; slightly hard; common fine manganiferous concretions; common fine woody roots; narrow boundary.
B1t	28–46 cm	Brown (7·5 YR 4/4–5/6) slightly stony clay with common faint to distinct paler brown and red mottles; stones as above, but generally larger; moderate medium to coarse blocky structure; very firm; very hard; few infilled worm channels; common woody roots; merging boundary.
B2t(g)	46–60+ cm	Strong brown (7·5 YR 5/6) slightly stony clay with common, increasingly distinct, pale brown and red mottles; moderate coarse blocky structure, with smooth shiny cleavage faces; very firm; very hard; fewer roots and channels.

Broadbalk wilderness (wooded)

A	0–10 cm	Very dark greyish brown (10 YR 3/2) stony loam with moderately developed fine sub-angular blocky and granular structure, the latter best expressed in the first 2 cm; stones comprise small sub-angular flints and a few rounded flint pebbles; slightly plastic; non-sticky; friable; abundant fine fibrous and common small woody roots; earthworms throughout profile; slightly calcareous; merging boundary.

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Eb	10–30 cm	Brown (10 YR 4/3) stony loam with moderately developed fine to medium sub-angular blocky structure and with inclusions of very dark greyish brown (10 YR 3/2) more granular material from the surface horizon; stones as above, together with a few very small chalk fragments; non-sticky; slightly plastic; friable; common fine fibrous roots and occasional larger woody roots; very slightly calcareous; narrow irregular boundary.
Eb/Bt	30–40 cm	Brown (7·5 YR 4/4) stony loam to clay loam; stones as above, up to medium in size; moderately developed medium to fine blocky structure; slightly sticky; slightly plastic; friable; few fine fibrous roots; very slightly calcareous; merging boundary.
Bt(g)	40–60+ cm	Reddish brown (5 YR 4/5) stony clay with common, faint, fine, paler brown and reddish mottling; stones as above; moderately developed coarse to medium blocky structure; sticky, plastic; firm; a few fine fibrous roots. (Note that the depth to this horizon varied from 30–75 cm in different holes.)

Broadbalk wilderness (stubbed)

A	0–15 cm	Dark greyish brown (10 YR 3/2–4/2) stony loam with a moderately developed fine sub-angular blocky to granular structure; stones mainly small sub-angular flints with a few rounded pebbles and small chalk fragments; non-sticky; slightly plastic; friable; abundant fine fibrous roots; earthworms throughout profile; slightly calcareous; narrow irregular boundary.
Eb	15–25 cm	Brown (10 YR 4/4) stony loam with a moderately developed fine sub-angular blocky structure; stones as above though more abundant; slightly sticky; slightly plastic; friable; fine fibrous roots common; calcareous; merging boundary.
B1t(g)	25–50 cm	Brown (7·5 YR 4/5) stony clay with common, fine, faint, strong brown and light brown mottling; stones as above; moderate medium blocky structure; sticky, plastic; firm; few infillings from horizons above; few manganiferous specklings; merging boundary.
B2t(g)	50–75+ cm	Strong brown (7·5 YR 5/6) stony clay with distinct, common, fine red (2·5 YR 4/6) and brown (7·5 YR 5/4) mottling, the latter particularly associated with ped faces; stones as above; moderate coarse blocky structure breaking to fine sub-angular blocky; sticky; plastic; firm; few fine fibrous roots; some manganiferous speckling.

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Soil Fumigation and Root-rots of Wheat

G. A. SALT

That fumigating soil could increase the yield of cereals was first shown at Rothamsted early this century when Russell and Hutchinson (1909) reported increases ranging between 20 and 50% in yield from plants grown in pots containing soil treated with toluene; responses they attributed to enhanced bacterial activity that increased the mineralisation of plant nutrients. However, in the field, carbon disulphide, toluene and formalin gave disappointingly small and inconsistent yield increases, which Russell (1914) attributed to the difficulties of fumigating soils efficiently in the field. The importance of soil-borne pathogens was only realised later, when Russell turned his attention to studying soil sickness of glasshouse soils, and got such improved growth after partial sterilisation that this was soon adopted as a standard practice.

The reason for resuming work on soil fumigation for cereals, after a lapse of 50 years, was given by Widdowson and Penny (1970), who used formalin drenches to try and gain information on the reason for cereal crops on some light soils promising well at first but failing during dry weather in June. In 1964 formalin trebled yields of spring wheat at Woburn, and greatly decreased the incidence of take-all *Ophiobolus graminis* Sacc. and cereal cyst nematode *Heterodera avenae* (Slope, 1966; Williams, 1969). In 1965 this work was extended to the heavier soil at Rothamsted, where take-all is sometimes severe, but where cereal cyst nematode and summer drought are much less harmful than at Woburn. Widdowson and Penny (1970) discussed both the effects of formalin and nitrogen fertiliser on the yields and N contents of spring and winter wheats, of barley and of grass. This paper describes the effects of these treatments on take-all and other fungal diseases in the wheat crops.

Methods and materials

The experiments were on adjacent fields, Little Knott, where 19 crops of cereals had been grown during the past 21 years, and Pastures, which had been in grass for ten years before it was ploughed and sown with spring wheat in 1964. The treatments, described in detail by Widdowson and Penny (1970) and Salt (1969), were formalin (266 gal of 38% formaldehyde in 4000 gal water/acre) applied by watering can, and four different amounts of calcium nitrate (Table 1). Spring wheats were sown in 1965 (Opal) and 1966 (Kloka), and in 1966 plots were such that effects of formalin applied in 1965 or 1966 could be compared with effects of applying it in both years or neither. In 1966 formalin was also applied during the autumn, before sowing winter wheat (Cappelle), again to plots that allowed residual effects to be compared with effects of newly applied formalin. In 1967 treatments were again applied during autumn before sowing Cappelle, but on Little Knott it was no longer possible to have plots that were given formalin each year or that had never had formalin. Samples, each containing about 50 plants from four separate 6-inch lengths of drill, were taken from each plot three times between April and July. After washing, each plant was scored for presence or absence of take-all, eyespot (*Cercosporella herpotrichoides*), sharp eyespot (*Rhizoctonia solani*), brown foot rot

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TABLE 1

Percentages of straws with roots infected by take-all in July 1965–68

Year	1965		1966			1967			1968			
Formalin	O	F	O	F	F	O	F	F	O	F	F	F
			1965	1965	—	1966	—	1966	1967	1967	—	1967
			1966	—	1966	1967	—	1967	1968	—	1968	1968
Cwt N/acre												
						Little Knott total infection						
0·0	99	38	96	100	19	46	74	100	77	100	64	100	73	98
0·5	92	30	77	94	12	30	84	98	48	86	36	85	56	50
1·0	92	24	49	90	0	11	61	98	66	96	18	68	97	40
1·5	91	38	62	86	4	25	60	100	62	87	13	53	80	41
						Little Knott severe infection						
0·0	69	9	44	90	7	28	7	94	35	34	28	56	26	30
0·5	55	9	44	72	12	3	26	74	2	75	4	19	27	9
1·0	38	4	13	59	0	3	0	28	36	50	0	23	47	12
1·5	52	15	33	54	0	17	2	69	6	26	0	13	45	0
						Pastures total infection						
0·0	6	0	84	62	15	27	92	96	74	54	31	29	32	57
0·5	0	0	54	59	28	32	69	100	71	81	32	65	55	56
1·0	0	6	42	50	46	16	76	84	51	80	72	33	19	30
1·5	0	0	46	34	5	10	69	100	88	78	13	76	76	54
						Pastures severe infection						
0·0	4	0	62	33	5	18	32	61	20	19	10	8	12	18
0·5	0	0	32	40	10	27	16	78	20	56	15	32	28	30
1·0	0	0	14	40	35	6	37	6	30	54	40	11	10	13
1·5	0	0	12	26	1	4	33	68	48	20	5	32	48	32

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(*Fusarium*), brown root rot (*Pythium*) and abnormal proliferating roots (*Heterodera avenae*). Severe take-all, affecting more than half of the root system sampled, was also recorded.

Results

Take-all on Little Knott, 1965–68. Formalin greatly decreased the incidence of take-all in June 1965 and its effect persisted and increased until harvest (Fig. 1). Nitrogen had no consistent effect on the proportion of infected or severely infected plants (Table 1), but greatly increased yields (Widdowson & Penny, 1970).

Formalin applied in 1966 decreased take-all even more than it had done in 1965, but less where it was also given in 1965 than where not. Where it was used in 1965 and not again in 1966, take-all was more prevalent and severe than where it had not been used at all (Fig. 1). Nitrogen greatly decreased both total and severe take-all, and decreased it most where formalin had not been applied in either year. Take-all was negligible with formalin plus 1·0 cwt N/acre in 1966, and grain yield averaged 42·5 cwt/acre, whereas with formalin in 1965 and no extra nitrogen in 1966, 90% straws were severely infected (Table 1) and yield averaged only 13·0 cwt/acre.

Formalin applied after ploughing in September 1966 decreased take-all in the winter wheat crop, but did not where applied to the stubble before ploughing (Fig. 2) and the mean effect, in contrast to previous years, was not significant. Where formalin was applied for the previous crop take-all was severe, and without extra N the crop almost failed, yielding only 4·4 cwt grain per acre. Nitrogen greatly increased grain and straw yields (Widdowson & Penny, 1970) but had no consistent effect on the incidence or severity of take-all (Table 1). Plots given formalin in 1966 and 1967 had more take-all and smaller yields than those without formalin in either year.

Formalin applied in September 1967 before sowing winter wheat decreased take-all next May, but later the disease developed more in fumigated plots, so that by harvest fumigation had increased disease incidence and severity (Fig. 1). A large increase in take-all after formalin in the previous season was evident on 2 May and remained until harvest. The most severe disease and smallest yield (17·5 cwt/acre) was again in unmanured plots treated with formalin in the previous season (Table 1). Nitrogen decreased the incidence and severity of disease, except where formalin was newly applied.

Formalin controlled take-all much better when applied in February before spring wheat than when applied in September before winter wheat. By contrast, the deleterious effect of formalin applied before the previous crop was as great, or greater, in winter as in spring wheat. This deleterious effect persisted for only one season, and where formalin was applied 2 or 3 years earlier there was less take-all and slightly larger yields than where it had not been used, but these differences were not significant at the 5% level.

Take-all on Pastures, 1965–68. Pastures soil was rich in nitrogen, and formalin and nitrogen affected yield much less than in Little Knott (Widdowson & Penny, 1970). Not only did plots without extra N yield much more than on Little Knott, but the potential benefit from formalin and nitrogen was lost because of lodging. In 1965 the spring wheat on Pastures had scarcely any take-all and the only benefit from formalin was a small increase in straw. Take-all occurred in the 1966 spring wheat crop, and its incidence was much decreased by formalin. In contrast to Little Knott, take-all was not increased by formalin applied in 1965 (Fig. 1). Nitrogen decreased the incidence and severity of infection (Table 1) especially in unfumigated soil, but yields were limited by lodging and were not increased by more than 0·5 cwt N/acre.

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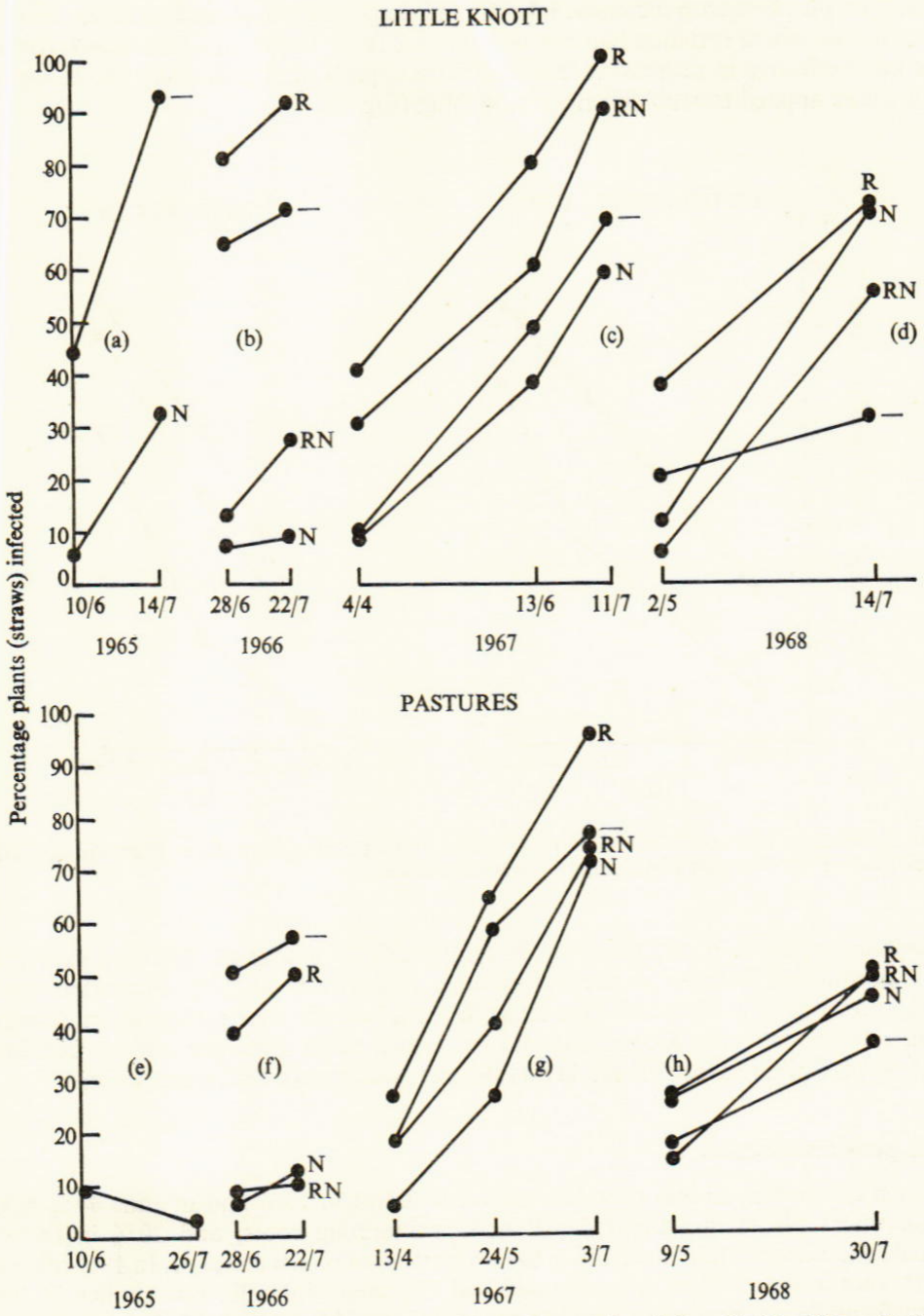

FIG. 1. Residual, direct and cumulative effects of formalin on take-all. R = Residual (formalin in previous year); N = New formalin in harvest year; RN = Formalin in previous and harvest year; — = None in harvest or previous year.

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In 1967 formalin affected take-all on Pastures as on Little Knott. Formalin applied before the previous crop increased take-all and depressed yields, and nitrogen decreased take-all only where formalin had not been given (Table 1). As on Little Knott, formalin was more effective in decreasing take-all where applied after ploughing and cultivating than where applied to stubble before ploughing (Fig. 2).

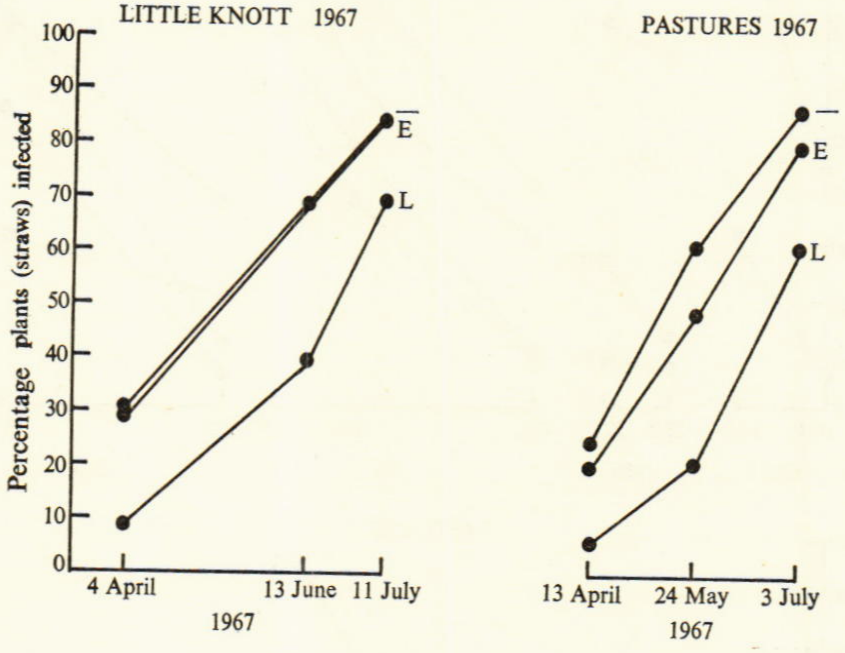

FIG. 2. Effect on take-all of formalin applied before and after ploughing. E = Formalin applied to stubble; L = Formalin after ploughing; — = No formalin.

Formalin applied in autumn 1967 had little effect on take-all but decreased grain yield, presumably because in the wet summer it increased lodging. Formalin applied for the previous crop increased take-all at harvest, but also increased yield, presumably because the poorer crop lodged less and so yielded more. Nitrogen had no consistent effect on take-all incidence (Table 1) and 0·5 cwt N/acre gave the largest yield.

Other pests and diseases

Cereal cyst nematode was prevalent on Little Knott in 1965 and in June 44% of the spring wheat plants in untreated soil had proliferating roots, and 20% in formaln treated soil. Nitrogen had no effect on the proportion of plants attacked. In 1966 attacked plants were fewer, 19% in untreated soil and 1% where formalin was applied in 1966. Where formalin was applied in 1965 but not again in 1966 there were 27% plants attacked, and 5% where formalin was applied in 1965 and 1966. These effects of formalin on *H. avenae* populations repeat those in the spring wheat at Woburn (Williams, 1969). *H. avenae* was less prevalent in the winter wheat on Little Knott in 1967 and 1968, and was not found in wheat on Pastures.

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Cercosporella herpotrichoides. Fewer plants were infected in Pastures than on Little Knott, and the percentages of straws infected by July were decreased by formalin (Table 2). In 1967 the drenches on stubble and after ploughing both decreased the amount of infection. In contrast to take-all and eelworm, eyespot was not increased by formalin applied for the previous crop; nitrogen had no consistent effect on eyespot.

TABLE 2

Percentage straws with eyespot

	July 1965	July 1966	April 1967	July 1967	July 1968
Little Knott					
No formalin	31	14	29	37	34
Formalin to stubble	—	—	19	37	—
Formalin after ploughing	12	3	15	31	27
Pastures					
No formalin	2	7	8	37	18
Formalin to stubble	—	—	7	15	—
Formalin after ploughing	1	1	7	24	13

Rhizoctonia solani affected fewer than 5% of the straws except in 1967 on Pastures, when 12% were infected in plots not treated with formalin, 8% where it was applied before ploughing, and 1% where it was applied after. Nitrogen had no effect.

Brown foot rot *Fusarium roseum* was also uncommon except in July 1967, on Little Knott, where 0·0, 0·5, 1·0 and 1·5 cwt N/acre gave 10, 14, 24 and 34% infected straws. Formalin had no effect.

Brown root rot was of two types. In one the roots were pale brown, watersoaked and many were filled with *Pythium* oospores. Most of the rotted portion was usually missing, leaving a tapering brown tip to the affected root. Pythium root rot was usually unaffected by nitrogen fertiliser or formalin. It was most prevalent in Little Knott during April 1967, when an average of 23% plants had a few roots infected, but usually fewer than 5% of plants were infected. The other form of root rot was more extensive and darker brown. Brown roots remained attached and did not contain oospores. *Fusarium avenaceum* and *Fusarium* (*sp.*), probably *F. tricinctum* were usually isolated. Usually few plants were affected, but the proportion increased with each increase in amount of nitrogen fertiliser and where formalin was applied. For example, on Little Knott in May 1968, 6, 21, 18 and 32% plants were affected in untreated, and 6, 30, 43 and 53% in formaldehyde-treated plots given 0·0, 0·5, 1·0 and 1·5 cwt N/acre respectively. This unusual prevalence on roots during May was not followed by brown rot of straw bases in July, which was wet and not expected to favour the development of brown foot rot symptoms. Except for cereal cyst nematode on Little Knott in 1965, these other diseases were of minor importance compared with take-all, and probably did not affect yields greatly.

Discussion

Effects of formalin on take-all are closely correlated with those on yield (Widdowson & Penny, 1970), with less take-all and increased yield in the first crop after application, but less yield and much more take-all when a second wheat crop is taken next year. Applying formalin for successive crops did not decrease take-all as much as the first application.

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Widdowson and Penny showed that formalin increased the amount of nitrogen assimilated by the crop, whether or not root pathogens were abundant. The amount of extra nitrogen assimilated was unexpectedly large; for example, on Little Knott in 1965 and 1966 the effect of formalin was approximately equivalent to giving wheat 1·0 cwt more N/acre. This benefit was probably derived partly from the healthier wheat using the reservoir of soil nitrogen more efficiently, and partly from the additional nitrogen mineralised by partial sterilisation of the soil (Gasser & Peachey, 1964; Jenkinson & Powlson, 1970; Williams & Salt, 1970).

The decreasing responses in yield to repeated formalin treatments were explained, partly at least, by Jenkinson and Powlson (1970), who found that soil from Pastures mineralized less nitrogen after a second than after the first fumigation, presumably because fumigation exhausts the reserves of nitrogen contained in living soil organisms. Thus, when nitrogen limits crop growth, a second fumigation will be less effective than the first in increasing yield, apart from any effect on plant pathogens. This difference between fumigated and unfumigated soils persists, for it was not only observed in Pastures soil three years after fumigation, but also in Butt Close soil, Woburn, five and a half years after treatment with formalin, and in Broadbalk 22 months after treatment with methyl bromide (Jenkinson & Powlson, 1970). In contrast to this persistent effect of fumigation on soil nitrogen reserves, there is evidence that the flush of additional mineral nitrogen released by fumigating field soils with various chemicals lasts only a matter of weeks, and is barely detectable after six months (Ebbels, 1968; Jenkinson & Powlson, 1970).

The extent to which soil nitrogen is exhausted by the crop taken after fumigation is shown dramatically on Little Knott by the near failures on unmanured plots, and the greatly improved yield on plots given increasing amounts of nitrogen fertiliser. On Pastures, with much larger nitrogen reserves, the residual effect of previous fumigation was much less harmful.

In addition to the depletion of nutrients, severe take-all also contributed to small yields by the second crop after fumigation. Lack of nutrients does itself increase the severity of take-all, but it seems that there must be other reasons for the take-all fungus developing so rapidly in the second crop after fumigation. It is easy to suggest that fumigation destroys antagonists that usually hold the pathogen in check, but this is difficult to prove. Winter (1942) showed that the growth of runner hyphae along wheat roots was stimulated by heating the soil or treating it with chloroform, sulphur dioxide, alcohol or tolulol, and he concluded that this stimulation resulted from the elimination of antagonistic organisms, which were restored to treated soils by inoculation with small amounts of unsterilised soil. Henry (1932) also concluded that antagonists to *O. graminis* were responsible for the disease rating of wheat seedlings decreasing in unsterilised but increasing in autoclaved soil as the temperature was raised from 13°C, where the disease rating was similar for both soils.

Fumigation behaves much as does introducing into a succession of cereal crops a crop that is not susceptible to take-all. There are much greater yields (with less fertiliser) and much less take-all in the next cereal than without any break from cereals, but smaller yields and more take-all in the succeeding crop than where cereals were grown continuously.

Suppressing organisms that inhibit the growth of the take-all fungus could explain some of the results of our experiments. However, for others it seems that the effects of formalin are rather on the extent to which the fungus survives in soil, and that the fungus has a greater chance of surviving between crops in fumigated than in unfumigated soils.

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Fumigation might aid the survival of the fungus in several ways. One could be by slowing the decomposition of crop residues, either because the crop is larger and removes more nitrogen from the soil, or because the soil saprophytes are fewer. Inoculum of the take-all fungus may be less effective from many diseased plants that die prematurely with rotted roots than from fewer plants that survive with larger slightly infected root systems.

It is worth comparing formalin with other fumigants used on field soils. Formalin and dazomet were better than chloropicrin, methyl bromide or 'D-D' in controlling take-all in spring wheat at Woburn (Williams & Salt, 1970), but formalin was the least effective in controlling nematodes. Except for 'D-D', all fumigants increased take-all in the second wheat crop grown the year after they were applied, but none by as much as formalin did. However, the adverse effect was counteracted by giving 1·8 cwt N/acre. It seems that it may be a common feature of fumigants that control take-all when first applied, to increase it in succeeding cereal crops, and for this deleterious effect to be decreased by applying more nitrogen fertiliser. The development of take-all in crops sown after soil fumigation must depend partly on the efficiency of the fumigant in killing the pathogen in crop debris in the soil. Ebbels (1970) showed that, in columns of soil in plastic tubes, only some of the mycelium in buried wheat straw was killed by fumigation. Formalin applied to the soil surface killed more *O. graminis* in the top 30 cm (12 in.) than in the 30 to 60 cm (12 to 24 in.) zone, where the fungus survived in more than half the pieces of straw. Chloropicrin injected at 15 cm (6 in.) killed more *O. graminis* than formalin in the top half of the columns but killed no more at greater depth. 'D-D' mixture had comparatively little effect and killed *O. graminis* inoculum for only a short distance below the point of injection at 15 cm (6 in.). Soil compaction and temperature in the soil columns probably differed from those in the field so extrapolation from these results must be done cautiously. However, fumigation in tubes of sieved soil is probably more efficient than in the field, and the results indicate that much of the take-all fungus in field soil may survive fumigation. The earlier wheat is sown the greater are its chances of becoming infected from viable fungus at greater soil depths. This would help to explain the poor control of take-all in winter wheat by formalin applied after ploughing, and the failure to achieve any control where applied before ploughing.

In two other experiments made at Rothamsted, fumigation failed to give the same control of take-all in winter wheat as described here with spring wheat. On Broadbalk methyl bromide applied under polythene sheets during October improved growth and decreased take-all in April, but by July there were more take-all infected plants in fumigated than in unfumigated soil (Salt & Corbett, 1969). On Claycroft field, formalin and dazomet both decreased take-all in April but the proportion of severely infected plants at harvest was decreased significantly only by dazomet (Ebbels, 1971).

Soil fumigation has largely failed to control other soil-borne diseases of cereals. Formalin was the only fumigant to decrease eyespot infection, probably because the way it was applied ensured its contact with superficial crop debris, which is the main source of infection (Cox & Cock, 1962). Ebbels (1970) confirmed this explanation by raking straw from treated and untreated plots at Rothamsted, and showing that the percentage of infective pieces was decreased by formalin but not by dazomet or 'D-D'. None of the fumigants tested decreased brown foot rot caused by *Fusarium roseum*, or brown root rot caused by *Pythium* spp. The survival of *Pythium* in crop debris or as resting spores in soil has not been recorded, but formalin or dazomet killed *F. roseum* in only one-third of the superficial pieces of straw (Ebbels, 1970). This suggests that the source of *Fusarium* infection, as of *C. herpotrichoides*, is mainly from surface litter. In forest nurseries, where the whole crop including most of the roots is removed each year,

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and where the light sandy soil is easily fumigated, formalin and dazomet both prevent *Fusarium* and *Pythium* infection of coniferous seedlings (Warcup, 1952; Salt, 1965). Failure to kill pathogens in agricultural soils is probably a mechanical problem of inefficient distribution of fumigant, rather than ineffectiveness of the chemicals, and sealing the soil surface with a plastic sheet after applying the fumigant would probably help to kill more fungi in the surface litter, where lethal concentrations of fumigant are difficult to maintain.

These results gave little hope of soil sterilants being used economically to control soil-borne diseases in intensive cereal growing, unless larger benefits can be obtained from cheaper materials. However, where cereals are grown in rotation with other crops, especially those producing larger returns per acre and susceptible to nematodes or fungi, there could be considerable benefit, for crops can benefit from a fumigation given some years earlier.

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Irrigation at Woburn—VII

H. L. PENMAN

Preamble

A Working Group of the Agricultural Research Council, looking at important future problems, used the term 'speculative' for research with no immediately obvious practical outlet either in agriculture or farming. The term is unfortunate in its association with gambles and guesses, but what it refers to, presumably, is that part of the research effort that is put into getting basic knowledge of the raw material, and of the enemies of the industry. Why the Research Council for the country's chief industry should seem to need special pleading for this kind of work is puzzling. Some of it pays for itself merely by occasional success in stopping expensive nonsense at source: some pays for itself in restricting or expanding the range of validity of empirical results from *ad hoc* experiments: much will pay for itself when the industry's techniques have caught up with research results sufficiently to be able to exploit them: and some can trigger a new technique, or greatly expand the use of a technique not previously thought necessary in a British environment. This, in essence, is the story of irrigation in Britain. Twenty years ago the area of farm crops irrigated was about 20 000 acres: now it is near 300 000 acres. The Rothamsted part in this had two components, visible and invisible. The visible part is in guidance material from the Ministry of Agriculture, Fisheries and Food in its *Bulletins* 138 and 202 and *Technical Bulletins* 4 and 16. The invisible part is, in some ways, even more important. The job needs water, and someone has to supply it, usually at times when demands from other consumers are greatest and reserves are least. Water authorities have been very ready—often eager—to try to meet this agricultural demand for water, and the Ministry has encouraged them to do so because both parties knew that the demand was based on 'speculative' research confirmed by well designed field experiments. For the same reason the Central Advisory Water Committee, in its thorough review of Britain's water resources and future needs, accepted this new use of water as a fair demand that Water Authorities must try to satisfy, and set up a Technical Sub-Committee to estimate the probable demand by 1980. The Committee Report (*Irrigation in Great Britain*, H.M.S.O. 1962) is, in design and effect, a short text-book on the subject, giving the bases, in physics and plant physiology, for water use by plants, showing why, where, and when summer water shortages occur, summarising the information then available on crop responses to irrigation (farm crops, vegetables, fruit) both in terms of agriculture (increased yield) and farming (increased profit), and estimating, against the then pattern of land use, the probable area that might be worth irrigating some day. Agriculturally—by including a lot of grassland—the area is 1 500 000 acres: more realistically—as farming—the area is about 500 000 acres, and this might well be reached in another ten years or so.

Part of the evidence used by the sub-committee came from the Woburn irrigation experiment: an account of the first nine years' results 1951–59 was published in three papers (Penman, 1962). A second group of three (Penman, 1970) completes the record, 1960–68. The two groups are numbered I to III, and IV to VI: these numbers will be used for simplicity in cross-references in this digest of 18 years of field measurements.

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Introduction

The raw materials of agriculture are the green plants, the soil, and the weather. For the water story it seems very obvious to start with 'What happens to the rain?' (Keen, 1939), but in this and a later review (Keen, 1940) it is almost as obvious that there is not much reward in the search for rain/growth relationships. Groping for reasons transforms the question to 'What happens to the sunshine?', which can be answered in a way that permits forecasting and backcasting. Ignoring meteorological complexity, the simple answer is: From a green farmscape about one-quarter of the sun's energy is reflected (Monteith, 1959): of the non-reflected energy, about half is used in evaporating water and the other half is used in various processes of energy transfer from the surface to the atmosphere. (To give scale, during a fine mid-summer week in S.E. England the average solar radiation income is near 480 cal cm^{-2} day^{-1}, and with one-quarter reflected there are 180 cal cm^{-2} day^{-1} each for evaporation and for other sinks. At 600 cal g^{-1} for the energy of vapourisation, the estimated evaporation rate is 0·3 g cm^{-2} day^{-1}, or 3 mm per day in the equivalent rainfall unit). The more exact working answer needs some quantification of the energy transferred in the other processes and this can be achieved with knowledge of air temperature, air humidity, wind speed, and duration of bright sunshine (used indirectly as a measure of cloud cover). These are the elements measured—as routine—at weather stations, and thus it became possible to use past climatological records to calculate seasonal energy balances in a way that left evaporation as the only unknown. The result of a group effort was the production, by the Ministry of Agriculture, Fisheries and Food in 1954, of *Technical Bulletin* No. 4, on *The Calculation of Irrigation Need*. Figure 1 is from this bulletin, and shows how often summer rainfall (April to September, inclusive) falls short of calculated evaporation by more than 75 mm. The map is purely climatological: it cannot indicate how plant growth would be affected by attempts to manage this deficit. For this field experiments were needed, and after three years co-operative work with the British Sugar Corporation on two commercial farms (Penman, 1952), the Woburn experiment was started in 1951, with two objectives:

(i) Practical—to measure the response of ordinary farm crops to supplementary watering;

(ii) Speculative—to seek crop/weather relationships that might be applicable to other sites, crops and climates.

Basic ideas

Understanding of the field results, and their application to farm practice, will be greatly helped by a short account of some of the speculative ideas added to some basic concepts now generally accepted as a good working hypothesis in the physics and physiology of plant/water relations.

One physical boundary condition is that there is a large area of a short crop completely covering the ground, and that it is actively growing. (There are special problems in small areas, as in most field experiments; for tall crops, e.g. trees; for incomplete cover, e.g. sugar beet and potatoes at early stages; and for senescent or maturing crops.) When the water supply around the roots is adequate, the rate of water use is dictated by the weather, with plant factors having only a small effect, and soil factors negligible. This weather-determined rate is called the 'potential evaporation' or 'potential transpiration' rate and is given the symbol E_T (originally intended as the evaporation rate from a *turf* surface). In effect, E_T is the evaporation rate from an extended area of short grass kept

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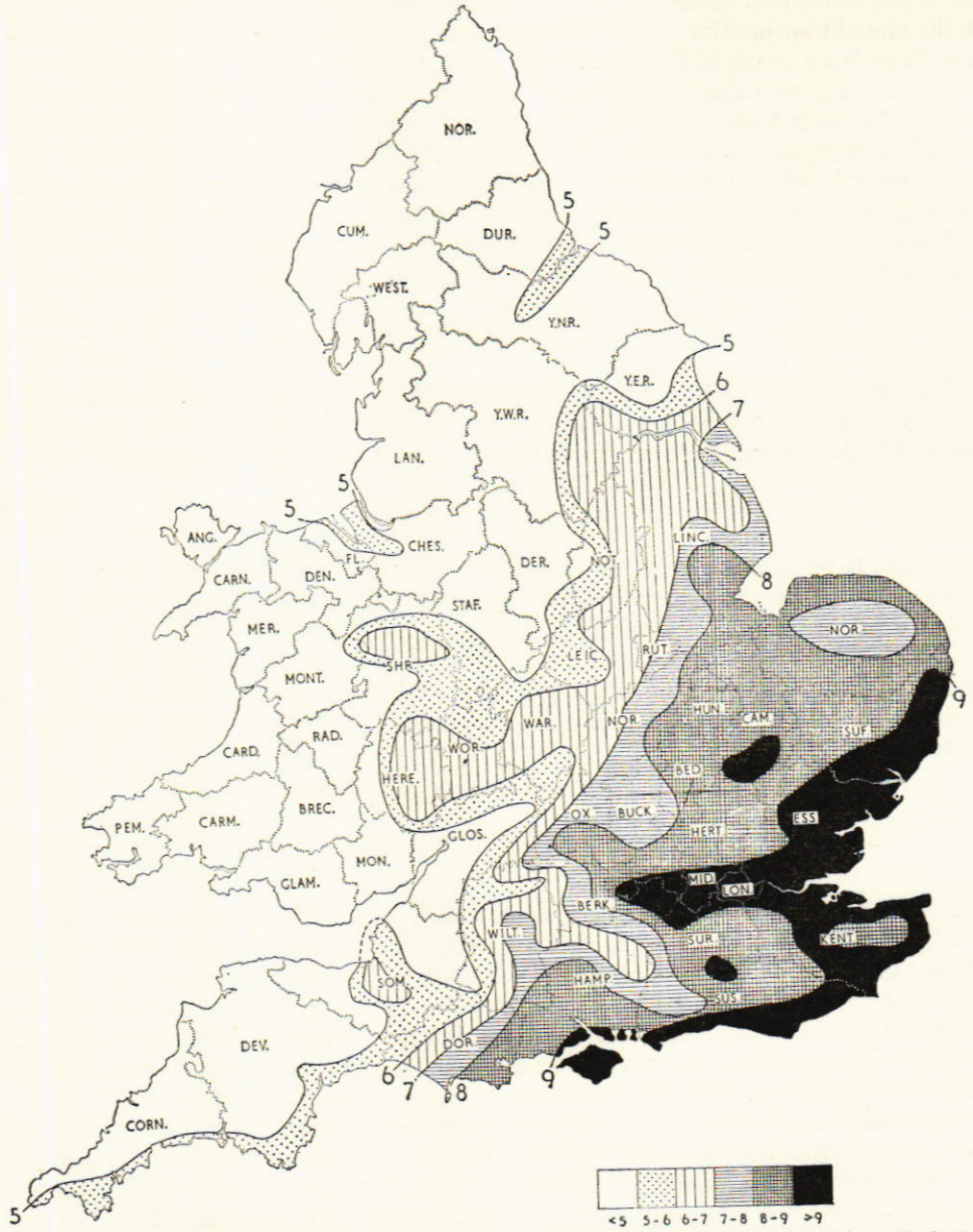

FIG. 1. Meteorological estimate of the frequency of irrigation need (years in ten). From: *Tech. Bull. Minist. Agric. Fish. Fd* No. 4, 1954. (H.M.S.O.)

in the vegetative phase of development, and it is not unreasonable to look for first tests of ideas on such a sward.

Starting from soil at field capacity, and in the absence of rain or irrigation, the transpiration stream will dry the soil at and near the plant roots, setting up stresses in both soil and plant. The soil stress may affect the ability of the roots to collect more water

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(i.e. a soil factor now comes in): the plant stress may affect the physiology, and, through it, the rate of transpiration, or the rate of assimilation. From field experience it is obvious that there is no check to plant growth in the early stages of soil drying, and thence it is an easy step to a simple hypothesis—at least worth a trial—that this period of unrestricted growth lasts up to a threshold of soil dryness, and that beyond the threshold there is a complete check. This threshold is defined quantitatively as a limiting deficit, D_l, as the rainfall equivalent of water that must then be added to restore the soil to field capacity. It represents the amount of water stored in the soil profile that the soil itself can contribute to plant growth: to get a measure of it, crop by crop, is the major technical objective in irrigation experiments. For rain, R, and irrigation, I, the deficit at any time is

$$D = E_T - (R + I) \tag{1}$$

and the simple hypothesis is that while D is less than D_l growth is unchecked, and while D is more than D_l *and still increasing* then growth is zero. An extension of the argument (see IV) leads to a value of the active evaporation contributing to plant growth as

$$E_A = E_T - D_m + D_l \tag{2}$$

where D_m is the maximum deficit reached during the period considered. Note that this implies that as the profile is rewetted—whatever the value of D—all evaporation is active. Again as another working hypothesis—one object of the work is to find field evidence—the growth rate, as botanical yield, is proportional to the potential transpiration rate when water supply is non-limiting, and the limiting deficit concept would add that total growth is proportional to the total active transpiration. Hence, with symbols representing totals,

$$Y = kE_T \qquad \text{while} \qquad D_m \text{ is less than } D_l \tag{3}$$

$$Y = k(E_T - D_m + D_l) \text{ otherwise.} \tag{4}$$

The effect of irrigation, I, is to decrease the deficit, so the maximum, D_{mI}, for an irrigated plot will always be less than D_{mO} for a control plot, but seasonal weather changes and the timing of irrigation operations will usually produce the result that $D_{mO} - D_{mI}$ is *less* than the irrigation applied (see Table 10). Further, for maximum irrigation, as planned, the value of D_{mI} will be less than D_l. For both reasons, the measured response, as $(Y_I - Y_O)/I$, will be less than k. In the limit, k represents the maximum possible response to irrigation, obtained when $D_{mO} - D_{mI} = I$ and $D_{mO} \geqslant D_l$.

It is easiest to estimate k for a ley, cut at intervals to give accumulated values of Y. Values of E_T and D_m are calculated from weather records, and the only unknown is D_l. There are various ways of estimating D_l, but it can usually be done by inspection and adjusted by trial until a plot of Y against E_A gives a straight line. For a ley, cut perhaps six times in a year, with four irrigation treatments (O, A, B, C, say), there will be 24 points to make coherent. Usually, some of these will correspond to duplicate treatments and will show a scatter inescapable in field measurements: if the processed points fit a straight line with not much more than the same scale of scatter, then the processing can be regarded as successful, the slope of the line can be used as a value of k (the maximum possible response), and the value of D_l chosen to achieve coherence can be accepted with some confidence. This is the quantity needed to give practical guidance to farmers.

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The experiment

The ideas and equations will become much more real when the symbols turn into numbers, and in the next section the results for a ley, 1951–53, will be examined in some detail.

The experiment was set out in the south-east corner of Butt Close on the northern edge of the Lower Greensand at Woburn. The area was roughly 150 × 100 m, with a good open exposure to west and north, and also to the east except for a few tall trees, but was very sheltered all along the south side: it is probable that estimates of water need were somewhat smaller than they would have been for a more exposed site, and the meteorological frequency of irrigation need a little smaller than Fig. 1 predicts. The soil, a sandy loam, contains enough clay to give coherent clods in the top foot, but below it is loose unconsolidated sand. The infiltration capacity is not very great, and care was needed to avoid run-off when irrigating row crops.

The area was divided into four series (I to IV) each divided into 12 plots giving three-fold replication of four possible watering treatments. Though it was expected that there would be important interactions between water and fertiliser treatments the degrees of freedom available were too few to permit much variation (and the plots were too small anyway). Each crop was given the basic fertiliser treatment conforming to recommended good practice, with one variant introduced by splitting plots. It was usually an extra nitrogen dressing. Weather records were taken on the site or at the farm about 350 m away. The unit of time was the week, ending on Monday morning, and irrigation instructions were received at Woburn on the Wednesday.

For the first 15 years, up to 1965, Series IV carried some sort of ley and the other series had varied three-course rotations. From 1966 onward the emphasis was on management, with series IV and I used for a long term potato experiment on cyst nematodes, while the other two were used for *ad hoc* experiments, including trials of the dwarfing compound CCC (Humphries, 1970). Some of the results 1966–69 are relevant to the present survey, but not all.

The general watering policy was that each unit block of four plots should carry an unwatered plot (*O*), and one fully irrigated (*C*) on which the aim was to keep the deficit at less than 2·5 cm: occasionally, unavoidable delays allowed the deficit to increase beyond 2·5 cm, and sometimes rain quickly decreased it to zero with a surplus as 'estimated drainage'. The other two plots, *A* and *B*, had regimes intermediate between *O* and *C*; for annual crops one would be at the *C* rate early in the season and the other zero, and then the 'early' plot would get no more and the other would get the same treatment as *C* 'late' in the season. The division between 'early' and 'late' was usually based on some easily recognised phase in crop development, e.g. ear emergence for cereals, flowering in potatoes and beans.

Leys

Particular, 1951–53 (Table 1). The seeds mixture was broadcast on 24 April 1951 with components: Italian ryegrass (6), S26 cocksfoot (16), S100 white clover (4) and Canadian Alsike (2). Next day basal fertiliser was applied: P_2O_5 and K_2O at 0·6 cwt acre^{-1}. There was no nitrogen applied until after the first cut on 11 July, and then it was as 'Nitro-Chalk' at two intensities: N_1, 0·15; N_2, 0·30 cwt N acre^{-1}. These dressings were repeated after the second and third cuts, 13 August and 4 September, but not after the fourth cut on 9 October. In 1952 the basal PK dressing was applied on 21 March—no nitrogen—and the N_1 and N_2 dressings applied after the first four cuts (29 April, 19 May, 16 June,

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TABLE 1

Grass/clover, 1951–53

Sown 24 April 1951. $N_1 = 0{\cdot}15$, $N_2 = 0{\cdot}30$ cwt acre^{-1} N per application

Year	Number of N applications	N_1 Best yield t ha^{-1}	N_1 Grass/clover *O*	N_1 Grass/clover *C*	N_1 Response t ha^{-1} cm^{-1}	k_1	N_2 Best yield t ha^{-1}	N_2 Grass/clover *O*	N_2 Grass/clover *C*	N_2 Response t ha^{-1} cm^{-1}	k_2	k_2/k_1
1951	3	6·4	2·4	1·4	0·23	0·38	7·4	7	2·3	0·16	0·48	1·26
1952	4	10·4	3·9	2·3	0·29	0·25	11·0	27	8	0·31	0·26	1·04
1953	1 + 6	12·2	1·9	1·6	0·08	0·28	13·5	5	3·9	0·13	0·32	1·13

General note, for all tables and figures.

1 t ha^{-1} ≅ 8 cwt acre^{-1}

1 t ha^{-1} cm^{-1} ≅ 1 ton acre^{-1} in.$^{-1}$

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9 July) but not after the fifth, sixth and seventh cuts (11 August, 9 September and 3 October). In 1953 the basal dressing was applied on 17 March, and nitrogen dressings, N_1 and N_2, applied on 27 March. As before, 'Nitro-Chalk' was given after the first six cuts (13 May, 8 June, 3 July, 4 August, 24 August and 16 September). The final cut was on 29 October, and the site was ploughed on 24 November.

There was randomisation of treatments in 1951, but no change was made in 1952 or 1953, either in fertiliser treatment or in watering treatment: thus treatments called ON_1, or CN_2, refer to the same plots (and plants) throughout the three years. Yields were estimated from fresh weight, measured on the plots, and dry matter contents determined on samples. After plentiful rain or irrigation the dry matter content was about 20%: after drought and no irrigation it was about 35%. From small samples, *rough* estimates were made of the grass and clover contents, too crude for safe use in quantitative analysis, but useful in providing numbers to match visual impressions of sward composition. This, summarised as the ratio in annual totals (Table 1) varied throughout each summer on a given plot, and was clearly changed by nitrogen treatment (more N, less clover) and by watering treatment (more water, more clover). Because of the seasonal changes and the interactions of treatments it was thought—quite wrongly, as it happened—that a mixed ley of this kind would not be amenable to any profitable attempt to extract crop/weather relationships. Accordingly, the site was ploughed, and re-seeded in April 1954 with a pure stand of cocksfoot (see next section). This gave some very valuable relationships, and the doubts of 1953 were removed when it was found (Penman, 1967–68) that the same analytical treatment could be applied to the results of Stiles and Williams (1965) who had done almost exactly the same experiment on irrigation of a mixture of ryegrass and white clover at the Grassland Research Institute. The inference—steadily becoming more confident as experience accumulates—is that within a given system of well-managed farming, the composition of a crop does not greatly affect the total yield of dry matter, and it is not important whether the division is, as in a ley, between species, or, as in a monoculture, between components, e.g. roots and tops, or grain and straw. (Sugar beet is a notable exception: it seems to produce more dry matter for a given radiation income than any other crop in the world.)

For the present survey it has seemed worthwhile to re-examine the results for 1951–53 in the same way as was done for the cocksfoot 1954–59, so providing something new, avoiding repetition, illustrating the degree of success attainable in handling equation (4) diagrammatically, and, incidentally, raising the same scientific problems as emerged from all the other years and crops.

As part of the general survey for leys the results appear at the top of Table 2. Here the yield for Y_I is that from the plots receiving most water: in one out of the six responses given it was not the maximum yield. For the detail leading to these annual totals and responses it is necessary to know a little about the history of management and weather.

1951. The engineering was not completed soon enough, and the first irrigation was applied later than desired. Some was applied before the first cut (there was no nitrogen discrimination at this stage) and more before the second cut on the *C* plots. These then had no more (*A* and *B* had a little) and it is best to compare only the *O* and *C* plots for 1951. The cumulative yields appear on Fig. 2a plotted against E_T from a zero time taken as at the first cut, when yields for N_1 and N_2 were the same—at zero nitrogen dressing. The starting point for the lines drawn is at the time of the first irrigation when the unknown amount of growth would be the same for all plots, irrespective of later treatments.

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1952. There was no need for irrigation until after the second cut, so the first two sets of points on Fig. 2b represent replicate treatments. After the second cut there was a dry period of eight weeks, and then enough rain to satisfy water need. The zero time is the date of the last cut in 1951.

1953. The first nitrogen was applied before the first cut, and the first irrigation between the first and second cuts. After several weeks of need, the summer weather was broken by three weeks of unusually heavy rain after mid-June. For the *C* plots this gave a total of 'estimated drainage' of 14 cm up to the time of the last cut, nearly half of it between cuts 3 and 5. The zero time is near the date of the last cut in 1953.

The weather distribution in 1951 was fortunate, in that all the irrigation need came before the crop was established, and the important aspects of the results can be picked out without any knowledge of maximum or limiting deficits. From the second cut onward, the sets of three points are colinear, and within each pair the lines are parallel. The

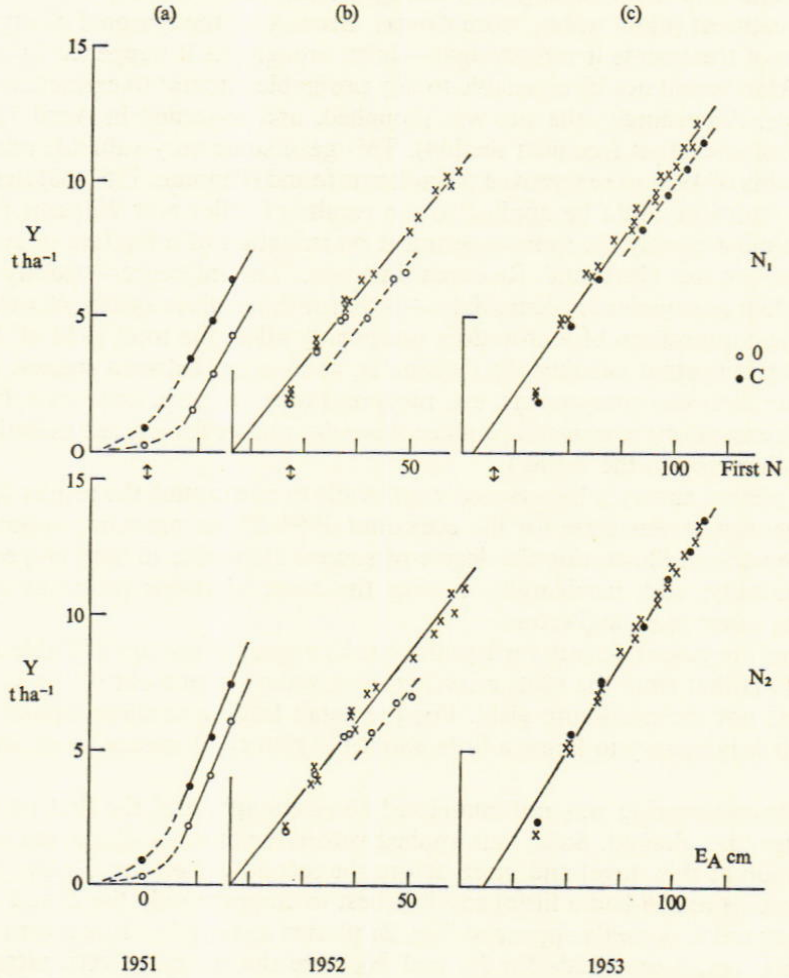

FIG. 2. Cumulative growth curves: grass/clover 1951–53. Points for control plots (*O*) and most-irrigated plots (*C*) are distinguished only where they have a special interest. The abscissa is accumulated *active* evaporation, estimated from the date of the first cut in 1951, and using $D_l = 2{\cdot}5$ cm for N_1, and $D_l = 3{\cdot}8$ cm for N_2. ($N_2 = 2 \times N_1$.)

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slopes are $k_1 = 0{\cdot}38$ t ha^{-1} cm^{-1} for N_1, and $k_2 = 0{\cdot}48$ t ha^{-1} cm^{-1} for N_2, both very large values indicating that the crop grew rapidly and made very efficient use of solar radiation. The irrigation response is revealed in two ways. First, the vertical separation shows the increase in yield produced by irrigation, and at the last cut of all this is $Y_I - Y_O$ of Table 2. Divided by the amount applied ($I_c = 8{\cdot}9$ cm), the responses of 0·23 and 0·16 t ha^{-1} cm^{-1}, for N_1 and N_2 respectively, are much smaller than the values for k_1 and k_2. Second, the horizontal separation represents a time benefit in getting the crop established. In E_T units, the values are about 6 cm for N_1 and about 3 cm for N_2: between the second and third cuts these intervals represent about 22 and 11 days. Qualitatively, the results are coherent. The greater horizontal spacing for N_1 implies greater sensitivity to soil moisture deficit, and hence greater response to irrigation, but quantitatively the size of the difference is surprising. There was *no* nitrogen applied until after the first cut, and yet by the time of the second cut the differential effect of two rates was fully established, over a period in which there was enough rain to get the unirrigated plots fully established. Were it worth seeking here, the explanation might be found in the grass/clover ratios at the second cut. They were: ON_1, 0·9; CN_1, 0·5; ON_2, 5·5; and CN_2, 0·8. As already noted, these ratios are very approximate, but, crude as they are, they indicate that the clover was dominant on three of the treatments and almost absent from the fourth (ON_2). The 'greater sensitivity to soil moisture deficit' may be that clover is more sensitive than grass.

The first cut in 1952 was for equal treatments since early September 1951, with the yields from the N_2 plots only a little greater than those from the N_1 plots (averages: N_1, 1·97; N_2, 2·14 t ha^{-1}) (Fig. 2b). Throughout the summer the ratio of growth rates never really exceeded this ratio (final values of Y_I: N_1, 10·4; N_2, 11·0 t ha^{-1}), and because the differential response was small it is unlikely that the absolute effects were very great. When Y was plotted against $E_T - D_m$ there was evidence of coherence in B and C results ($I_B = 8{\cdot}6$ cm; $I_C = 13{\cdot}0$ cm) with A and O results clearly anomalous. The coherence was improved by using as limiting deficits, 2·5 cm for N_1, and 3·8 cm for N_2. In plotting, for Fig. 2b, the last three points for A treatment were omitted (for clarity), and the last three for O treatment were not put in until the straight lines had been fitted to the remaining 22 points. Except for the values at the first cut, the straight lines drawn fit the observations very well, and, extrapolated back to $Y = 0$, the apparent zero time coincides with the date of the last cut in the previous year. The deviation of the first cut values always occurs—it is obvious again for 1953—but it is not an effect of irrigation.

The slopes of the lines are: N_1, 0·25 t ha^{-1} cm^{-1}; N_2, 0·26 t ha^{-1} cm^{-1}, as the maximum possible response to irrigation: the real responses (Tables 1 and 2) are greater. The beginnings of an explanation of this apparent absurdity can be seen on the diagram. From cut 3 to cut 5 the growth on the O plots was barely measurable, i.e. there was no response to the rain that fell during the period (8 cm in 56 days). From cut 5 on, growth was resumed, and at the same rate as the well watered B and C plots. For the N_1 line, with slope 0·25 t ha^{-1} cm^{-1}, the displacement of the control plot results is 1·3 t ha^{-1}, corresponding to an unused amount of rainfall of 5 cm. This is another benefit from irrigation: for a crop that would otherwise go senescent in a period of near drought, irrigation not only produces its own response to water paid for, but also keeps the crop in a state that it can respond to rain, which is free.

The important change in management in 1953 was that nitrogen dressings were applied in spring, before the first cut, and after six of the seven cuts, equal in amount to the total applied in the previous two years. The processing of results was as for 1952, with the same limiting deficits (N_1, 2·5; N_2, 3·8 cm) but the lines were drawn through the points

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before plotting the results for the fully watered *C* treatment. The reason—now considered unjustified—was a suspicion that the small yields on the *C* plots were caused by leaching of nutrients during the wet period between cuts three and five. The leaching idea was abandoned, first because there is no hint of it in the N_2 results, and, second, because the CN_1 results lie below the line from the second cut onward: a poor first or second yield, or a faulty measurement of either, would be carried forward into all later totals. The final four points for CN_1 lie on a line parallel to the full line, with slope $k_1 = 0{\cdot}28$ t ha^{-1} cm^{-1}. For N_2, $k_2 = 0{\cdot}32$ t ha^{-1} cm^{-1}, and here the ratio k_2/k_1 is nearer the value it had in 1951 (Table 1). The intercepts on the axis at $Y = 0$ are near the zero time corresponding to the date of the last cut in the previous year: they are also near the date of the first application of nitrogen. Farm practice is to apply spring dressings of nitrogen when spring growth is seen to have started, so this second near coincidence may be more meaningful than the first.

General

Grass, 1954 onward. Table 2 gives yields without irrigation (Y_O) and the responses to irrigation (Y_I–Y_O) for 12 years. For all entries, Y_I is the yield from *C* plots that had

TABLE 2

Response of leys to irrigation, 1951–65

Dry matter, t ha^{-1}

$N_1 = 0{\cdot}15$, $N_2 = 0{\cdot}30$, $N_4 = 0{\cdot}60$ cwt acre^{-1} N per application

Year	I cm	Y_O			$Y_I - Y_O$			$(Y_I - Y_O)/I$		
		N_1	N_2	N_4	N_1	N_2	N_4	N_1	N_2	N_4
		Mixture: 2 grasses, 2 clovers								
1951	8·9	4·3	6·0	—	2·1	1·4	—	0·23	0·16	—
1952	13·0	6·7	7·0	—	3·7	4·0	—	0·29	0·31	—
1953	14·2	10·3	11·8	—	1·2	1·7	—	0·08	0·13	—
		New crop: S 37 Cocksfoot								
1954	7·4	4·0	6·5	—	0·0	−0·1	—	0·0	0·0	—
1955	19·6	4·6	6·8	—	3·3	3·4	—	0·17	0·18	—
1956	9·9	7·0	10·2	—	2·0	2·3	—	0·21	0·23	—
1957	13·7	—	7·9	10·5	—	2·3	2·1	—	0·17	0·16
1958	10·9	—	9·2	11·5	—	0·8	0·1	—	0·07	0·01
1959	17·3	—	3·4	4·3	—	4·2	5·6	—	0·24	0·32
		New crop: S 22 Italian ryegrass								
1960	8·4	—	10·5	12·0	—	2·1	3·1	—	0·25	0·35
1961	15·2	—	5·6	5·7	—	3·1	6·5	—	0·20	0·43
1962–64		Lucerne (Table 3)								
		New crop: S 22								
1965	3·8	—	—	12·0	—	—	0·0	—	—	0·0

most water applied. There were changes in the intensity of nitrogen dressings, and in the basic fertiliser too, but these will be noted as they become relevant. In nine of the 12 years the response was at least half-a-ton per acre of dry matter, and in some years very much better. The three years of zero response—1954, 1958, and 1965—differed in rainfall distribution. In both 1954 and 1958 there were intermittent relatively dry periods, and, with no long-range weather forecast as a guide, each dry period was treated as the

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beginning of real summer weather. Invariably application of irrigation was followed by rain: by the end of 1958 the *C* plots had received more irrigation and rain than they could hold but the estimated leaching seems to have done no harm to the absolute yield, but may have decreased the response to nitrogen a little. During 1965 the summer rain was very uniformly distributed and there were only two occasions when irrigation was called for—but some response was expected. One factor that may have contributed to failure was the intrusion of volunteer lucerne as a weed: by the end of the summer the infestation was too severe to justify continued cropping into 1966, and beyond, as planned, and the experiment was ended.

Cocksfoot, 1954–59. The crop was sown on 7 April 1954 in a dry period, and *all* plots were irrigated early in May to get it established. Basal fertiliser, and nitrogen had been applied the day before sowing (P_2O_5, 0·6; K_2O, 1·2; N_1 and N_2, 0·15 and 0·30 cwt acre^{-1}). There were six cuts in 1954, and N_1 and N_2 were applied after each cut except the last (4 November). For 1955 (seven cuts) and 1956 (six cuts) there were the same spring dressings and N applications after cutting. A change was made in 1957. The half plots previously at rate N_1 were now given four times as much (labelled N_4): the N_2

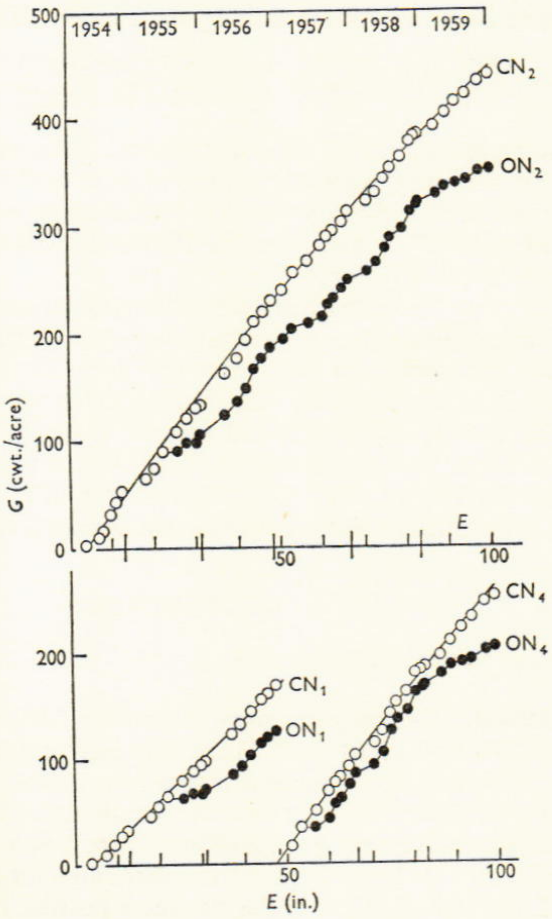

FIG. 3. Cumulative growth curves: S 37 Cocksfoot 1954–59. The abscissa is accumulated potential evaporation. (Note the units.) From: *J. Agric. Sci.* (1962), **58**. (Cambridge U.P.)

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plots continued as before. Yields had been good, and it was suspected that the crop might be exhausting potash reserves, so, in 1958 and 1959, supplementary potash was added to 6/12 plots. There was weed invasion in the sixth summer and the experiment was ended after the cut on 9 September. The unirrigated plots were very dry and hard: they were irrigated on 14 September (2 cm) and this made ploughing possible a week later (another benefit from irrigation).

Details of analysis are in II and only a few need repetition. Figure 3 reproduces Fig. 2 of II, the top half showing the total growth for CN_2 and ON_2 plots, over a period of six summers and five winters, plotted against accumulated potential transpiration. The first obvious result is that the average gain from irrigation was near 25%. The line drawn, obviously a good general fit, has a slight curvature towards the end (effect of weeds?). For any summer the line somewhat distorts trends, particularly in the first year. Using only the results from the *C* plots, the individual values of k_2 are:

1954, 0·40; 1955, 0·28; 1956, 0·33;
1957, 0·21; 1958, 0·33; 1959, 0·21 t ha^{-1} cm^{-1}

The full analysis, applied to all treatments, was given (Fig. 3 in II) for two years only, using values of limiting deficit: N_1, $D_l = 2{\cdot}5$ cm; N_2, $D_l = 3{\cdot}8$ cm; N_4, $D_l = 5{\cdot}1$ cm. (These have illusory precision—read them as 1, 1½ and 2 inches.) The values of *k* derived were:

1955, $k_1 = 0{\cdot}20$; $k_2 = 0{\cdot}27$ t ha^{-1} cm^{-1}
1957, $k_4 = 0{\cdot}28$; $k_2 = 0{\cdot}24$ t ha^{-1} cm^{-1}

The lines then drawn, representing $Y = kE_A$, repeated the behaviour of Fig. 2: for 1957 the intercepts at $Y = 0$ were very nearly the same and close to the origin at the time of the last cut in 1956 (as for 1952 and 1951); for 1955 the intercepts were the same for both N_1 and N_2, but to the right of the origin (as for 1953 and 1952) and very close to the time of the spring application of nitrogen.

There was a similar contemporary experiment at the Grassland Research Institute, Hurley (Stiles & Williams, 1965). A ryegrass/white clover sward, established in 1951 came into an irrigation experiment for four years 1956 to 1959. One of the treatments was the same as the Woburn *C* treatment, and, by chance, the nitrogen treatments were the same as the N_1, N_2 and N_4 at Woburn, and used the same material. There was also a zero treatment, N_0. From weather records at Kew Observatory values of E_T were calculated for the period (Penman, 1967–68), and used to plot total yield against total E_T. The result was a set of straight lines similar to that of Fig. 3 and the general slopes were:

$k_0 = 0{\cdot}18$; $k_1 = 0{\cdot}20$;
$k_2 = 0{\cdot}24$; $k_4 = 0{\cdot}30$ t ha^{-1} cm^{-1}.

The Woburn and Hurley results agree very well.

Italian ryegrass, 1960–61. The crop was sown in October 1959, and a basal dressing of N, P and K was applied on 1 April 1960. There were eight cuts to 8 November, and dressings N_2 and N_4 (as before) were applied after each cut except the last, and muriate of potash was applied to half plots after the first and fourth cuts. There was an excellent yield from the control plots and a very good response to irrigation. Simple trial showed that $D_l = 5$ cm was adequate for both nitrogen treatments, and, for the larger K dressing represented in Table 2, the derived values of the maximum possible response to irrigation were:

$k_2 = 0{\cdot}34$; $k_4 = 0{\cdot}40$ t ha^{-1}

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The measured responses, in the table, are smaller, as expected. There was some evidence of a rather complex interaction between K treatment and response to irrigation, discussed, but not clearly resolved, in Paper V.

In 1961 the best yield was less than was expected, perhaps because of a strong invasion of *Poa annua* that started at the beginning of July. It was killed by drought on the control plots, but persisted on the watered plots, though very little appeared in the cut grass. The slope of the line $Y = kE_A$ for the larger nitrogen and potash dressings was $k_4 = 0{\cdot}27$ t ha^{-1} cm^{-1}. The measured value of $(Y_I - Y_O)/I$ was 0·43 t ha^{-1} cm^{-1}.

Here is another example of the enhanced benefit from irrigation, because unwatered plots could not exploit rain.

Because of the weeds, the plots were ploughed up, and, after three years under lucerne, another grass crop was sown in 1965.

Italian ryegrass, 1965. The experience with fertilisers in the earlier experiments on this particular soil suggested that a change in practice was desirable to maintain the large yields obtained by irrigation. In the event it was not given a thorough test, but the applications, for 1965, were: Basal, applied immediately before sowing, March 1965: P (0·6 cwt acre^{-1} P_2O_5); NK compound at two rates (0·5 or 1·0 cwt acre^{-1} N; 0·5 or 1·0 cwt acre^{-1} K_2O). There were five cuts, and the NK compound, at the two rates, was applied after each cut except the last.

As already noted, the small amount of irrigation had no effect, there was no weather problem in getting the crop established, the yield was good, and from the slope of the line $Y = kE_T$ the value of k was 0·46 t ha^{-1} cm^{-1}, representing very efficient fixation of solar radiation.

Lucerne 1962–64 (Table 3). The lucerne came in the ley sequence on series IV (see Table 2), after ryegrass. The fertiliser treatments balanced those given to the grass. They were:

TABLE 3

Response of legumes to irrigation

Dry matter, t ha^{-1}

Lucerne, 1962–64

		Y_O				Y_I			
		K_1		K_2		K_1		K_2	
Year	I cm	N_0	N_1	N_0	N_1	N_0	N_1	N_0	N_1
1962	8·9	5·73	5·87	5·78	6·09	6·23	6·59	7·25	6·90
Response t ha^{-1} cm^{-1}						0·06	0·08	0·16	0·09
1963	5·1 early 3·2 late 8·3 early and late			No response		Average yield = 7·9 t ha^{-1}			
1964	1·3 early 2·5 late 6·4 early and late			No response		Average yield = 9·5 t ha^{-1}			

Clover, 1963–65

Year	I cm	Y_O	Y_I	Response t ha^{-1} cm^{-1}	Notes
1963	7·0	2·13	3·23	0·16	Crimson C. 1 cut only
1964	11·4	6·08	8·78	0·24	Dorset Marl. 3 cuts
1965	3·8	8·52	8·54	0·00	Dorset Marl. 3 cuts

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P_2O_5 at 0·6 cwt acre^{-1} on all plots; $N_0 = 0{\cdot}0$ and $N_1 = 0{\cdot}3$ cwt acre^{-1} of N as 'Nitro-Chalk'; $K_1 = 0{\cdot}3$, and $K_2 = 0{\cdot}9$ cwt acre^{-1} of K_2O as muriate of potash. Fertiliser was applied two weeks before drilling the seed, and the NK treatments were repeated after each cut, including the last on 3 October 1962. In 1963 and 1964 there was spring application of NPK, and only K dressings after cutting.

As for the first ley, in 1951, all the irrigation in 1962 was applied before the first cut, and on all treatments the benefit was clearly established by the time of the first cut, with K_2 plots just a little better than K_1. Later behaviour was different: for three treatments the value of $Y_I - Y_0$ decreased at both the second and third cuts, to about half of its value at the first cut. The exception was the N_0K_2 treatment, which maintained its early response.

The yield gap established in 1962 was maintained in 1963 and 1964 (no response to irrigation), and plotting of total yield against total E_T (V; Fig. 6) gave three groups of 3, 3 and 4 points, each group fairly fitted by a straight line, the three lines very nearly parallel with slope 0·26 t ha^{-1} cm^{-1}, but not colinear. The obvious winter gaps correspond to a period without growth from the end of November to mid-March. A rough estimate of limiting deficit for the established crop was: $D_l \simeq 11$ cm. This confirms world experience, that lucerne is a deep-rooting crop and can survive drought better than any other fodder crop.

Clover, 1963–65 (Table 3). The clover was grown as part of a three-course rotation. In each year it followed barley, in 1963 as a newly drilled crop (April), and in 1964 and 1965 as crops undersown in preceding barley crops selectively irrigated.

As for the 1951 ley and the 1962 lucerne, irrigation of the Crimson Clover in 1963 helped establishment, there was a good response at the first cut, and then no more: the experiment was abandoned. The combination of sunshine and irrigation increased inter-node spacing so much that the cutting completely defoliated the crop, and there was no significant recovery, even with irrigation.

The Dorset Marl had basal PK fertiliser applied in February 1964 and 1965, there were four irrigation treatments and these were distributed so that the plots watered in the barley year got least in the clover year. There was no doubt about the excellence of response in 1964, but there is some confusion in results for 1965. The balancing of watering treatments between 1964 and 1965 meant that the least watered plots in 1965 had a better start because they were irrigated in 1964.

The results for 1964 and 1965 gave 24 yields (three cuts, four watering treatments, two years), and plotting Y against $E_T - D_m$ gave a well distributed set of points lying closely about a straight line of slope $k = 0{\cdot}23$ t ha^{-1} cm^{-1}—the expected maximum possible response to irrigation. (The two points for crimson clover conformed well.) This is the same as the measured response in 1964 (Table 3), and implies that the limiting deficit for clover is small, and that there was a period during 1964 in which the unwatered plots were not making full use of the rain they received. A provisional value of D_l is 2·5 cm, but it may be smaller.

Crops grown in rotation

Introduction. Formal analysis is more difficult for annual crops: there is only one yield per treatment per year, the yield may not be the total botanical yield, and there is uncertainty about the length of the growing season (particularly the end—harvest may be delayed). Nevertheless it seemed worthwhile attempting to fit the standard equation

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$Y = k(E_T - D_m + D_l)$ to results, circumventing the uncertainty in E_T in various ways to reach acceptable estimates of D_l, the limiting deficit needed to guide good irrigation practice, and of k, the maximum possible response to irrigation, either for the whole crop, or for the part of economic value.

Potatoes

Early potatoes, 1951–53, 1960–62 (Table 4). These were not truly early potatoes. Planting dates ranged from 13 March to 25 April, and harvest from 10 to 31 July. In the fertiliser treatments there was basic P and K (more in 1960–62 than in 1951–53), and two intensities of nitrogen ($N_1 = 0{\cdot}5$, $N_2 = 1{\cdot}0$, 1951–53; $N_1 = 0{\cdot}6$, $N_2 = 1{\cdot}2$ cwt acre^{-1}, 1960–62). There were only two watering treatments (*O* and *C*) during 1960–62: another management variant was imposed, in a comparison of normal cultivation with weed control by chemical means. The result was not successful; all yields and responses were decreased by about one-third. Results in Table 4 are for normal cultivation.

TABLE 4

Response of potatoes to irrigation

Tubers as harvested, t ha^{-1}

Early—(1) Ulster Chieftain, 1951, 1952, 1953

Year	I cm	Y_O N_1	Y_O N_2	$Y_I - Y_O$ N_1	$Y_I - Y_O$ N_2	$(Y_I - Y_O)/I$ N_1	$(Y_I - Y_O)/I$ N_2	Approx. $4k$ N_1	Approx. $4k$ N_2
1951	5·6	9·3	9·5	9·5	11·4	1·7	2·0		
1952	6·9	14·7	15·2	9·1	11·5	1·3	1·7	1·8	2·0
1953	5·1	24·5	29·5	4·9	6·6	1·0	1·3		
(2) Arran Pilot, 1960, 1961, 1962									
1960	3·8	22·7	26·0	4·5	6·5	1·2	1·7		
1961	10·2	14·6	17·2	18·7	20·2	1·8	2·0	1·8	2·1
1962	7·6	7·2	7·0	6·0	8·5	0·8	1·1		
Maincrop—(1) Majestic, 1954, 1955, 1956									
1954	5·6	34·5	44·0	−2·0	−2·2	−0·4	−0·4		
1955	16·0	26·5	28·0	20·1	15·3	1·3	1·6	1·8	2·0
1956	1·3	34·8	38·3	1·5	1·2	1·2	0·9		

(2) Maris Piper and Pentland Dell, 1966 onward, on the same sites

Year	I cm	No fumigant: Cysts Y_O	No fumigant: Cysts Y_I	No fumigant: No cysts Y_O	No fumigant: No cysts Y_I	Fumigant: Cysts Y_O	Fumigant: Cysts Y_I	Fumigant: No cysts Y_O	Fumigant: No cysts Y_I	General response
1966	7·6	27·4	22·0	44·5	35·0	38·2	33·6	46·4	42·5	−
1967	10·8	8·9	10·5	22·5	22·3	20·2	28·1	31·0	37·7	+
1968	4 or 6	19		26		30		33		0
1969	6·5	6	9	←worst		best→		42	50	+

Responses were good in all six years, yields being doubled in 1951, 1961 and 1962, but the last result must be received with caution. The seed tubers were damaged by frost before planting, growth was patchy, and absolute yields were poor. Some of the measured responses are very close to the theoretical maximum, again indicating that the value of D_l is small, and that in 1951, and 1961, and probably in 1952 and 1960 the secondary benefit of irrigation was operative: it kept the crop in a state to exploit all the rain that fell.

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Majestic, 1954–56 (Table 4). The same fertiliser treatments as for 1951–53 were imposed on a basal dung dressing of 15 tons acre^{-1}. There were two wet years in three, giving a small negative response in 1954 (wet), a very big response in 1955 (dry), and a small response in 1956 (wet). The negative response is considered later.

In analysis of these results and those for 1951–53 it was found—and noted as fortuitous at the time—that all could be fitted by the same straight lines of $Y = C(E_T - D_m + D_l)$ with two values of C_1 and C_2 corresponding to N_1 and N_2, using the same value of $D_l = 2{\cdot}5$ cm for both varieties. These slopes are given under 'Approx. $4k$' in Table 4, and, if the implicit assumption is accepted, then the slopes for dry matter production are: N_1, $k_1 = 0{\cdot}45$; N_2, $k_2 = 0{\cdot}50$ t ha^{-1} cm^{-1}, about the same as for a fully established grass ley in its first year.

Main crop, 1966 onward (Table 4). After 15 years under ley, Series IV was only slightly infested with potato cyst-nematode, whereas Series I had carried several potato crops, and some plots were heavily infested. The sites are now used for a long-term experiment in nematology, comparing resistant and susceptible varieties of potato, in succession and alternating, with and without soil fumigation, and with and without irrigation. An undistorted summary is unattainable, but the selected material in the fourth section of Table 4 may not be too misleading. For 1966–68 average yields of the two varieties show an unexpected negative response to irrigation in 1966, a good response in 1967, but somewhat smaller than expected, and no response in 1968, as expected (only average yields are given). For 1969 the best (Maris Piper, the resistant variety on fumigated cleaner plots) and worst (Pentland Dell, non-resistant on non-fumigated infested plots) yields are given. The best yields, and the response to irrigation, are about the same as for Majestic potatoes in 1955.

The behaviour in 1966 repeated that of the main-crop in 1954, but with bigger negative responses. The explanation offered is that in 1966 the combination of early watering and rain produced estimated drainage through the irrigated plots and none through the control plots, in amount 2·5 cm by the end of June, 3·7 cm by the end of August, and 5·3 cm by harvest time. The effect was about equivalent to halving the nitrogen dressing (1·2 cwt acre^{-1} N in basal NPK). The same effect probably occurred in 1954: colour contrasts in foliage early in July 1954 provoked the query 'Leaching?'. The early leaching may be the more important.

Sugar beet. Table 5 includes results from experiments, 1948–50, on commercial farms (Penman, 1952) where two farmers co-operated with the British Sugar Beet Research and Education Committee: at least one treatment was based on weather records collected on or near the site, and this provides the entry in the table.

Management was very much the same throughout. There was basal PK, sometimes agricultural salt, and two intensities of nitrogen fertiliser, with $N_2 = 2 \times N_1$. Values were: 1948–50, $N_1 = 0{\cdot}4$; 1951–56, $N_1 = 0{\cdot}4$; 1957–59, $N_1 = 0{\cdot}6$; 1963–65, $N_1 = 0{\cdot}75$ cwt acre^{-1}.

During the 15 years there were good to excellent responses in six, the outstanding returns coming in years of late summer drought (1949, 1955, 1959 and 1964). There were five years in which there were small negative responses on the plots that got most water, perhaps because of leaching, but the evidence is not conclusive, and there may be some other factor to look for. The results given are for sugar yields: they fluctuate greatly from year to year, and the total botanical yield probably changed as irregularly, so there is little hope of any successful synthesis that will give the important parameters

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TABLE 5

Response of sugar beet to irrigation

Year	I cm	Sugar, t ha^{-1} Y_O N$_1$	Y_O N$_2$	$Y_I - Y_O$ N$_1$	$Y_I - Y_O$ N$_2$	Selected $(Y_I - Y_O)/I$ N$_1$	Selected $(Y_I - Y_O)/I$ N$_2$
			Milford (Surrey)				
1948	6·6	—	8·4	—	0·1	—	—
1949	21·0	4·5	4·4	1·0	1·2	0·05	0·06
			Kesgrave (Suffolk)				
1949	14·8	3·8	3·9	3·0	2·4	0·20	0·16
1950	10·2	6·5	6·9	1·8	1·1	0·18	0·11
			Woburn (Beds.)				
1951	8·6	5·5	7·1	0·2	0·8	—	0·09
1952	14·2	5·9	7·0	1·4	0·5	0·10	—
1953	9·2	10·1	10·9	−0·1	−0·5	—	—
1954	3·3	5·2	5·9	0·0	0·0	—	—
1955	16·2	4·1	4·5	1·4	1·0	0·09	0·12
1956	3·6	7·5	8·4	−0·6	−0·2	—	—
1957	9·2	7·5	8·0	−0·5	−0·1	—	—
1958	4·6	5·2	6·2	−0·5	−0·5	—	—
1959	18·6	7·8	7·2	3·2	3·8	0·17	0·20
1963	8·3	7·8	8·0	0·1	0·8	—	0·10
1964	10·2	6·8	6·4	1·5	3·5	0·15	0·34
1965	3·8	8·1	8·1	−1·1	−0·3	—	—

in the total growth equation $Y = kE_A$. An attempt to do so on the results for 1963–65 (VI, Fig. 1a) gave a value of $k \simeq 1$ t ha^{-1} cm^{-1} for total dry matter, and if sugar represents 40% of total dry matter, then $k_S \simeq 0{\cdot}4$ t ha^{-1} cm^{-1}. The year to year variation can be eliminated by using the ratio S/S_m, where S_m is the maximum yield in the range of treatments, and S is the actual yield. This, plotted in Fig. 1b, in VI, for three years, is repeated here as Fig. 4, but now includes 12 years of Woburn results for all O, B and C plots. The few A plot values are omitted for clarity. The ordinate is the ratio S/S_m, as the average of the two nitrogen treatments. The abscissa is the maximum deficit, D_m, after the middle of July. The diagram is informative in several ways. Five of the O points lie below 90%, i.e. in five out of 12 years failure to irrigate decreased yield by more than 10%. Six of the B and C points are below 100%. (The lowest, at 0·91, is for 1965.) The roughly fitted line passes through $D_m \simeq 10$ cm at 100% and this offers a useful guide to irrigation management—keep the deficit at less than 10 cm from mid-July onward. The slope of the line is 0·045 cm^{-1}. For a good sugar yield of 8 t ha^{-1}, this would correspond to $k_S \simeq 0{\cdot}36$ t ha^{-1} cm^{-1}. This is a large value, confirming what is in Table 5: at its best the sugar production by a sugar beet crop is almost as good as the total dry matter production of a ley. The maximum values of $(Y_I - Y_O)/I$ anywhere in Table 5 are 0·20 (N$_1$, Kesgrave, 1949), 0·12 (N$_2$, Woburn, 1955), 0·17 and 0·20 (N$_1$ and N$_2$, Woburn, 1959), and 0·33 (N$_2$, Woburn, 1964).

In several years, early irrigation produced obvious response in top growth, but the benefit did not persist through to harvest. It is difficult to offer advice that will improve on the practice of one successful grower: give the crop a good soaking in mid-July (about 5 cm) and then no more unless the late summer is exceptionally dry.

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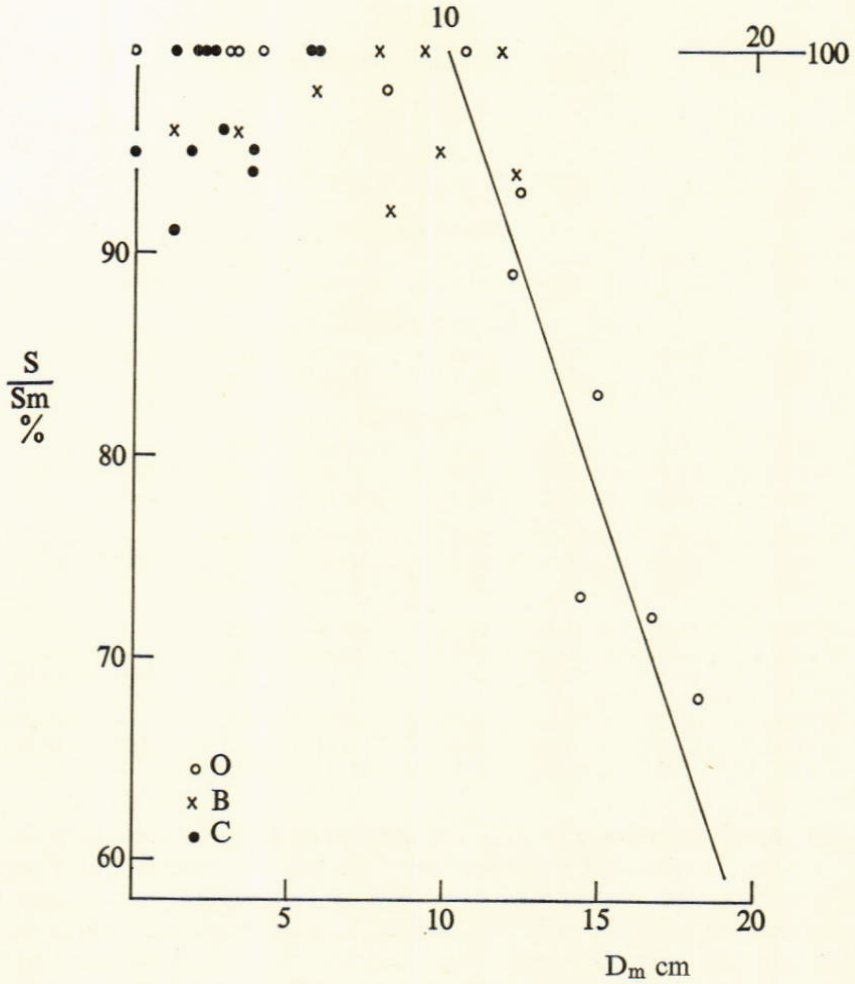

FIG. 4. Sugar yield (S) as a fraction of the best yield (S_m) plotted against maximum deficit after mid-July. 1951–59; 1963–65.

Barley (Table 6). The cereals have proved the least amenable to formal analysis, and even after 11 years of irrigation experiment on barley guidance on practice is based largely on impression. The results for 1968 in Table 6 are for interest only: an experiment on soil fumigation included irrigation as a variable, and there was some response where chloropicrin showed its efficiency as a nitrogen fertiliser.

For the ordinary experiments, 1951 onward, there was basal PK plus nitrogen at $N_1 = 0{\cdot}2$ and $N_2 = 0{\cdot}4$ cwt acre^{-1} up to 1956, and again 1960–62, but for 1963 and 1964 the rates were 0·3 and 0·6 cwt acre^{-1}. In the first two courses, barley came after potatoes in 1951 and after sugar beet in the other five years. In 1960 it came after a bean crop. In 1961, 1962 and 1963 the barley was in a sequence that started with early potatoes, half cultivated, half treated with weedicide, then some plots were drilled with trefoil, later ploughed in as green manure, and then came the barley. The results in Table 6 are for the sequence: potatoes cultivated, and no intervening trefoil. In 1963 and 1964 the barley was undersown with clover.

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TABLE 6

Response of barley to irrigation

Grain yield (dry matter), t ha^{-1}

Year	Variety	I cm	Yo N_1	Yo N_2	$Y_I - Yo$ N_1	$Y_I - Yo$ N_2	Selected $(Y_I - Yo)/I$ N_1	Selected $(Y_I - Yo)/I$ N_2
1951	Plumage Archer	8·1	2·71	3·76	0·91	0·39	0·11	—
1952	,, ,,	7·3	2·71	2·89	0·12	0·51	—	0·07
1953	,, ,,	2·0	2·96	3·74	−0·04	−0·14	—	−0·07
1954	Herta	4·6	3·91	4·60	0·22	−0·10	0·05	—
1955	,,	3·5	3·96	5·06	0·10	−0·14	—	—
1956	,,	6·6	3·08	3·90	0·56	0·44	0·08	0·07
1960	Proctor	5·1	2·12	2·73	0·35	0·39	0·07	0·08
1961	,,	8·2	2·71	3·27	0·09	0·21	—	—
1962	,,	8·9	2·05	2·60	0·84	1·07	0·09	0·12
1963	Proctor	7·0	1·78	2·72	0·45	0·76	0·06	0·11
1964	Maris Badger	5·1	3·00	3·90	0·24	0·03	0·05	—
			N_0	N_1	N_0	N_1		
1968	Maris Badger	3·2	1·08	2·93	−0·03	−0·04	No fumigant	
	,, ,,		3·04	3·33	0·29	0·14	Chloropicrin	

From the four years results for Proctor (and Maris Badger in 1964 conforms) it seems that the response of barley to irrigation can be interpreted if it is assumed to behave as a grass crop up to the time of ear emergence, i.e. the best grain yield will be achieved if the deficit is kept at less than 4 cm up to this stage: what happens after has little detectable effect. Visual checks on the results for the first six years show no extreme contradiction to this specification. For example, there was a good yield of Herta in 1955 when the condition was satisfied in both treatments, and, though there was severe drought afterward, there was no response to irrigation. (As a technical point, for both barley and wheat, irrigation was stopped when the farm manager considered that the risk of lodging was too great to accept.)

In general, responses were small, with erratic interactions of watering and nitrogen. Again as an impression, water and nitrogen seem to be interchangeable—but nitrogen always produces a response.

There is no information in Table 6 relevant to the other parts of the experiments of 1961–63. A quotation from Paper VI (p. 96) may suffice: 'Preceding management of the potato crop probably had no effect on the growth of the barley. Trefoil increased the yields, certainly at the smaller nitrogen dressing, probably at the larger one, halved the response to nitrogen, and may have increased the response to water.'

With great uncertainty, an approximate value of k_g is near 0·16 t ha^{-1} cm^{-1}, for the grain, for both nitrogen treatments.

Spring wheat (Table 7). During 1957–59 wheat came in a normal rotation, after sugar beet, and was given basal PK fertiliser plus nitrogen at intensity $N_1 = 0{\cdot}4$ cwt acre^{-1} of N. Other rates, then and later, were N_2, N_3 (and N_4) at 2, 3 and (4) $\times$ N_1. The second group includes results for experiments in 1966 and 1967 on the dwarfing compound, CCC (Humphries, 1970). Four intensities of nitrogen fertiliser were used but as the fourth was rather far outside the specification of 'recommended best practice' results are given for three only. The values given are averages with and without CCC.

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TABLE 7

Response of spring wheat to irrigation

Grain yield (dry matter), t ha^{-1}

Year	Variety	I cm	Y_O N$_1$	Y_O N$_2$	Y_O N$_3$	$Y_I - Y_O$ N$_1$	$Y_I - Y_O$ N$_2$	$Y_I - Y_O$ N$_3$	Selected $(Y_I - Y_O)/I$ N$_1$	Selected $(Y_I - Y_O)/I$ N$_2$	Selected $(Y_I - Y_O)/I$ N$_3$
1957	Peko	8·1	2·70	2·75	—	0·28	0·76	—	—	0·09	—
1958	,,	3·8	2·59	2·94	—	−0·14	−0·24	—	−0·04	−0·06	—
1959	,,	11·9	1·94	1·81	—	1·11	1·38	—	0·09	0·12	—
1965	Opal	3·8	3·48	4·04	3·90	0·21	0·42	0·21	0·06	0·11	0·06
1966	Kloka	7·6	2·68	4·08	4·31	0·58	0·44	1·13	0·08	0·06	0·15
1967	,,	10·2	3·79	5·02	4·56	0·37	0·45	1·18	—	0·04	0·12

Except in the wet summer of 1958, when there was a small negative response to a small amount of irrigation, spring wheat responded to irrigation, by more than 50% in 1959. There is much less evidence available than there is for barley, and generalisation is based on impression. Like barley, spring wheat should be treated as a grass until ear emergence: unlike barley, it seems to be somewhat sensitive to later deficit, and a guide to action would be: keep the deficit at less than 4 cm up to ear emergence and thereafter do not let it increase above $E_T/4$—measured from sowing date.

Analysis of the results gives a very tentative value of k_g for wheat as near 0·24 t ha^{-1} cm^{-1}, for the grain, for N > N$_1$: it is much less at the smallest nitrogen dressing, and apparently the wheat needed nitrogen at rate N$_2$ to be able to respond to irrigation.

Two general points in crop–weather relationships are worth noting here. First: spring wheat responds to water—positively—like any other grass crop, and a droughty summer is not the best for getting maximum yield out of a healthy crop. Second: the 1967 crop was healthy: there were straw yields too, and for the best nine plots the average total dry matter at harvest was 12 t ha^{-1}, even after losses during maturation. This is as good as is obtainable from a well managed ley or a very good potato crop.

Beans (Table 8). The first three years of spring beans had the fertiliser variant of dung at 12 tons acre^{-1} applied on half-plots in winter (D_1). The seed was drilled with a basic PK fertiliser. For the second three years the intention was to use winter beans, but drilling was not possible in autumn 1960, and the crop drilled in autumn 1961 failed. The 1968 crop had no PK, but was given nitro-chalk (four treatments) and a dwarfing compound (B-Nine, two treatments). The entries in Table 8 are for the zero treatments for N and B-Nine.

Analyses of the two sets of results (1957–59; 1960–68) give concordant values of limiting deficit near $D_l = 4$ cm, but the value of k_g, for grain, was near 0·14 for 1957–59, and 0·17 t ha^{-1} cm^{-1} for 1960–68: this is another way of indicating that yields were about 20% better in the second period.

Except in 1958 and 1968, when the summers were wet and little irrigation was applied, the responses were very good, and almost the same as the theoretical maxima inferred from the analysis. This confirms that the limiting deficit is indeed small, but if it is not to be made vanishingly small then in all five years of good response the irrigation was needed to keep the crop vigorous enough to respond to rain. Other crops have shown this susceptibility occasionally, but none so frequently, and the derived values of D_l may be over-estimates, and the conflict between real performance (as in Table 8) and predicted

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TABLE 8

Response of beans to irrigation

Grain yield (dry matter), t ha^{-1}

Year	Variety	I cm	Y_O D_0	Y_O D_1	$Y_I - Y_O$ D_0	$Y_I - Y_O$ D_1	$(Y_I - Y_O)/I$ D_0	$(Y_I - Y_O)/I$ D_1
1957	Spring tick	10·2	1·47	1·74	1·77	1·47	0·17	0·14
1958	,, ,,	2·5	1·91	1·79	0·09	0·05	0·04	0·02
1959	,, ,,	11·4	1·02	1·12	1·61	1·50	0·14	0·13
1960	Winter, RSQ	9·0	2·40	—	1·24	—	0·14	—
1961	Spring tick	11·4	1·41	—	1·65	—	0·14	—
1962	,, ,,	8·3	2·23	—	1·33	—	0·16	—
1968	Tarvin	3·3	2·95	—	0·16	—	0·05	—

maximum best becomes perhaps rather more severe. (At present, August 1970, at the end of a fairly dry summer, the bean crop is showing the same behaviour. On ordinary experiments, and on the unwatered control of the irrigation experiment, the crop is poor and only about 20 in. tall. The irrigated plants are about 40 in. tall.)

Discussion

(Table 9)

The value of successful irrigation is that it provides the water of a wet summer in the sunshine of a fine one. No one doubts that there is no need for it in wet summers such as 1954, 1958 and 1963, or that it could be beneficial in extremely dry summers such as 1955 (after June), 1959 and 1964, but in between there is uncertainty. Arbitrarily (i.e. based

TABLE 9

Fractional increases in yield (%) for maximum irrigation

Year	Year of 'need'?	Grass/ clover	Grass	Lucerne	Clover	Early potatoes	Maincrop potatoes	Sugar beet	Barley	Spring wheat	Beans
1951	+	23	—	—	—	120	—	11	10	—	—
1952	+	57	—	—	—	76	—	7	18	—	—
1953	0	14	—	—	—	22	—	−5	−4	—	—
1954	0	—	0	—	—	—	−5	0	−2	—	—
1955	+	—	50	—	—	—	90	45	−3	—	—
1956	0	—	22	—	—	—	3	−2	11	—	—
1957	+	—	29	—	—	—	—	−1	—	27	120
1958	0	—	9	—	—	—	—	−8	—	−8	5
1959	+	—	123	—	—	—	—	53	—	76	158
1960	0	—	18	—	—	25	—	—	14	—	52
1961	+	—	114	—	—	118	—	—	6	—	116
1962	0	—	—	26	—	122	—	—	41	—	60
1963	+	—	—	0	52	—	—	10	28	—	—
1964	+	—	—	0	44	—	—	55	1	—	—
1965	0	—	0	—	0	—	—	−4	—	10	—
1966	0	—	—	—	—	—	−12	—	—	11	—
1967	+	—	—	—	—	—	24	—	—	9	—
1968	0	—	—	—	—	—	10	—	−1	—	5
1969	+	—	—	—	—	—	19	—	—	—	—
Limiting deficit (in.)		1–1½	1–2	4	1	1	1	4	1½	1½	1½
Estimated k for whole crop t ha^{-1} cm^{-1}			0·3	0·3	0·2	0·5	0·5	1·0	0·3	0·4	0·3

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on judgement) *Technical Bulletin* No. 4 defined a year of irrigation need as one in which the excess of potential evaporation over rainfall is more than 3 in. for the period 1 April to 30 September. At Woburn this was expected to occur seven years in ten, but, as the second column of Table 9 shows, it happened only ten times in 19 years. This, though no more than an accepted variability in climatology, does mean that there have not been quite as many favourable proving years as expected. Even so, in 13 years at least one crop gave more than 20% increase in yield, in ten years at least one crop gave more than 50% increase, and in five years at least one crop yield was doubled. This is a fair enough summary of the field evidence, and has some legitimate propaganda value, but it is a little unfair technically. An alternative is: in five years at least one crop yield was halved because of lack of water, and one contributory factor was the failure of the crops to make full use of the rain they got. There is a need for another soil water parameter in growth studies, namely a deficit (or a water potential) within which the plant not only survives, but remains ready to respond to rain even when the growth rate is negligible or zero. It may be, as suggested in Paper V, that a promising index already exists (at least worth a trial) in the 'root constant' (Penman, 1949) introduced to account for the hydrology in terms of water balance, where growth is disregarded. At some stage, as the soil gets drier, the actual evaporation rate becomes smaller than the potential rate, and it may be at this stage, or a little beyond it, that the plant loses the ability to respond immediately to rain.

The conventional approach to responses, though it has been used in this survey, is not the best in water studies. For a given farming system there is a limit to the yield attainable when water supply is adequate, and it is the task of the remainder of agricultural research to raise this limit. Water cannot do so, but shortage of water can prevent a crop yield from reaching its optimum: part of the survey has been an attempt to show the scale of loss through the constant k. It has been called the 'maximum possible response to irrigation' (valuable if for no more than preventing too much being claimed for the technique—there's no magic or miracles in irrigation), but it is also a measure of the maximum possible loss in yield attributable to lack of water. With the very important qualification already sufficiently stressed (full use of rain), k as a measure of maximum disaster will always exaggerate because of the ability of the soil to store some water available for plant growth. Quantified through the limiting deficit, D_l, the value is not very different for all the crops in Table 9 (lucerne and sugar beet are the outstanding exceptions), at a value between 1 and 2 in. as rainfall equivalent. If this depends on the quantity of water held in the soil profile at low tension, then D_l will be bigger in soils heavier than the sandy Woburn loam: if—rather less likely, but possible—it depends on the depth of soil occupied by nutrients, then soil type may not be very important in determining the size of D_l. (N.A.A.S. experience on potatoes indicates that $D_l \simeq 1$ to $1\frac{1}{2}$ inches is best on a wide range of soils.)

The experiment had the advantage of first class management that got the best out of every crop. The values of k are a measure of this achievement, for, converted into dry matter equivalent of total botanical yield, they show no great spread (sugar beet excepted) about a general average near $k = 0{\cdot}3$ t ha^{-1} cm^{-1}: for a growing season with a total potential evaporation near 33 cm this corresponds to a total dry matter production near 10 t ha^{-1}, and an efficiency of fixation of solar radiation of about 80×10^{-4}. The efficiency of average British farming is near 35×10^{-4}. The point in these figures is that this efficiency (or the value of k) is a measure of the response to irrigation when irrigation is needed. The better the standard of farming, the greater is the return for added water.

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What happens to the water? Table 10 shows what might have occurred at Woburn, from April to November, with all quantities in centimetres per month. The first two lines give the rainfall and potential evaporation, and the third gives their monthly difference. The fourth line is a running total and represents the estimated soil moisture deficit at the end of each month: it reaches a maximum of 8 cm at the end of August (this would be D_m for the O treatment), and passes through zero in November to reach −5 cm at the end of the month (this would be 'estimated drainage' by that date). In line five is a possible C treatment, with irrigation amounts of 3 cm in both June and July, and after the obvious intermediate sixth, the seventh line gives the history of the managed deficit. The maximum is now only 3 cm, and it occurs at the end of June: the return to field capacity occurs in October (estimated drainage, 4 cm) and by the end of November the total estimated drainage is 11 cm, equal to that for the O treatment (5 cm) plus the added irrigation (6 cm).

TABLE 10

Idealised water-balance (cm per month)

		Month							
		April	May	June	July	Aug.	Sept.	Oct.	Nov.
	Rain R	5	5	5	7	6	5	7	8
O	Pot. evap. E_T	5	7	9	8	7	4	2	1
	$E_T - R$	0	2	4	1	1	−1	−5	−7
	Total $E_T - R = D$	0	2	6	7	**8**	7	2	(−5)
	Irrigation I	0	0	3	3	0	0	0	0
C	$E_T - (R + I)$	0	2	1	−2	1	−1	−5	−7
	Total $= D$	0	2	**3**	1	2	1	(−4)	(−11)

Accepting a very important unstated assumption, no irrigation water is consumed at Woburn. It starts in the Greensand aquifer under the plots and, after a complex route that makes it costly, it reaches the soil above the aquifer. Here it, or an equal amount, is stored until autumn rain is enough to wet the soil profile, and what was taken out from below in June and July is returned to source in October and early November, ahead of the main recharge through unirrigated areas. In the hydrological balance sheet for the area what was borrowed in summer is returned in autumn, and employed to grow a bigger crop in the interval. Suppose the crop to be grass with a limiting deficit of $D_l = 4$ cm, and consider growth from the end of March to the end of September. The value of E_T is 40 cm, and by the definition used the potential maximum yield is $40k$. For the O treatment the active evaporation ($E_A = E_T - D_m + D_l$) is $40 - 8 + 4 = 36$ cm and what would appear as Y_O in a table such as Table 2 is $Y_O = 36k$. For the C treatment D is always less than D_l and $E_A \equiv E_T = 40$ cm. Hence the corresponding entry for Y_I is $Y_I = 40k$. The derived measured response is then

$$(Y_I - Y_O)/I = (40k - 36k)/6 = 4k/6,$$

i.e. the measured response is less than the theoretical maximum by a factor 2/6, because 2 out of the 6 cm applied were not necessary: a total of 4 cm, applied either as two doses of 2 cm in June and July, or as a single dose in June—but *not* in July—would have served and given a full return equal to the maximum possible.

Here the assumption must be exposed. Does the diminished growth mean there is less water used? The best answer is: 'No—within limits,' so expressing the dominance of weather. The limits are imposed by plant and soil factors, and for the supposed crop

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and its seasonal water balance, as in Table 10, it is probable that the limit was reached at a maximum potential deficit of 8 cm. For a wetter summer the 'No' would be safe, and the hydrological inferences from Table 10 could be accepted. In a drier summer actual evaporation would be less than the potential, from the unwatered plots, for part of the time, because available water in the root zone was exhausted. Then the water balance in the upper part of Table 10 would be distorted in the sense that the actual maximum deficit would be less than the potential value (D_m), and autumn recharge of the aquifer would start sooner than predicted, and, relatively, the irrigation operation would seem somewhat disadvantageous.

The problem has some relevance to what farmers should pay for irrigation water, and a few more facts will be helpful. Current irrigation experiments at Rothamsted and Broom's Barn are beginning to provide these facts.

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Virus Diseases of the Honeybee

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Diseases resembling those now known to be caused by viruses were among the first to be noticed in honeybees, and they have been described by beekeepers since more than 100 years ago. Descriptions then made of 'paralysis' of adult bees and of some kinds of 'foulbrood' of their larvae correspond with those of paralysis, as it is still called today, and of sacbrood. In spite of the early diagnoses, however, the viruses causing these diseases were the latest, and may well be the last, of the common pathogens of honeybees to be identified. Most of this work has been done during the past decade.

Paralysis

Early history. The signs of paralysis in a bee colony were described originally as the emergence of many flightless moribund adult bees, usually termed 'crawlers', which often had distended abdomens and sometimes were also hairless, black and shiny. Some of these signs, or very similar ones, soon became associated with one or other of several micro-organisms discovered later, when the hunt for microscopic parasites of bees became popular, about 60 years ago. For example, *Nosema apis*, *Malpighamoeba mellificae* and *Acarapis woodi* were frequently found in colonies showing some of the signs previously ascribed to paralysis and became accepted as the cause of the symptoms. However, the terms 'Nosema disease', 'Amoeba disease' and 'Acarine disease', which are still commonly used, do not specify diseases or hint at symptoms; they were clearly invented to suit the names given to the three newly discovered parasites. In fact recent work has established that the parasites are often very numerous in seemingly healthy bees and colonies and, although *N. apis* and *A. woodi* have been shown to shorten bees' lives somewhat, none has been shown to cause overt signs (Bailey, 1968a). Nevertheless codes of the alleged symptoms of these parasitic infections of bees soon became accepted. Thereupon, the identity of paralysis became obscure and the name became a general term for various apparently uncommon diseases, mostly non-infectious, that seemed to have similar symptoms (Butler, 1943). Morison (1936) noted that only bees with all the symptoms of paralysis had basophilic cytoplasmic bodies in the cells of their hind-gut epithelium, whereas bees infected with the well-known parasites had not. However, the specificity of this sign was disputed soon after it was described because Lotmar (1940) found similar granules in moribund bees in Switzerland that were neither hairless not dark. As the Swiss bees were not infected with any known parasite, they were suspected to have been poisoned and the granules were associated with this.

Etiology. Burnside (1945) made the first successful experiments in the United States with one form, at least, of paralysis. The sick bees in nature were flightless and soon died, although few were hairless, black or shiny. Burnside serially passaged the disease nine times by spraying caged healthy bees with filtrates, free from bacteria and larger organisms, of extracts in water of sick individuals. The incubation period was 8 to 14 days in bees kept at about 23°C and the infected bees soon became trembly and flightless.

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Some were bloated but none became black or hairless. Bailey, Gibbs and Woods (1963) and Bailey (1965a) investigated the same or a very similar disease at Rothamsted where it had appeared spontaneously and very severely in a single colony. The sick bees were flightless and trembly and the trembliness was especially apparent when the bees were kept warm and compared with healthy individuals. More colonies were obtained showing the same severe symptoms from various parts of England. Dark, hairless bees were rare but a few sick individuals with bloated abdomens from the distension of their honey-sacs with liquid, invariably occurred within the colonies. In every way the disease seemed identical with that described by Burnside. Severe attacks were devastating. They were usually seen in summer when thousands of bees crawled and died, leaving the queen with a handful of attendant bees on the neglected combs of colonies that had appeared large and prosperous only a week or two previously.

Chronic bee-paralysis virus. Bailey *et al.* (1963) extracted a virus from paralysed bees by triturating them in water + carbon tetrachloride. They called this virus chronic bee-paralysis virus to differentiate it from another virus, acute bee-paralysis virus (see below), which they discovered at the same time. Later Bailey *et al.* (1968) found that extraction with water + ether followed by carbon tetrachloride was the most efficient method. Clarification of the extract at 8000 g for 10 minutes, followed by sedimentation at 75 000 g for $2\frac{1}{2}$ hours or precipitation with half-saturated ammonium sulphate, gives fairly pure preparation of anisometric particles that resemble prolate spheroids and range in size from 15 to 40 nm wide and 20 to 100 nm long. The average width of the particles, which contain nucleic acid of the ribose type, is about 21 nm and there are three components averaging 42, 52 and 61 nm in length, with sedimentation rates ($S_{20,w}$) of 97, 110 and 125 respectively. The smallest particles are the least infective. Paralysed bees from different sources in nature, and bees injected with fractions of extracts containing mostly large particles, all contain the three virus components in the same relative proportions. Between 10^{10} and 10^{11} particles can be extracted from one paralysed bee and the median lethal dose (LD 50) by injection into the haemolymph for adult bees is about 10^2 particles. The LD 50 of the virus when applied as a spray in water is between 10^9 and 10^{10} particles and when fed in syrup is more than 10^{10} particles. The sprayed virus probably infects via the tracheae and the true LD 50 is probably many fewer particles than all that are sprayed at a bee.

Bees infected by any method and incubated between 30° and 35°C become flightless and trembly about five to seven days after infection and die a day or so later. The lower the temperature the longer they take to die after first showing symptoms. Basophilic cytoplasmic bodies are strikingly evident in the cells of their hind-guts and some of the bees develop bloated abdomens caused by distension of their honey-sacs with liquid. These symptoms correspond exactly with those seen in nature.

Occurrence of paralysis. Much chronic bee-paralysis virus has been detected in bees found with paralysis symptoms and sent to Rothamsted from Australia, China, Mexico, the U.S.A., Scandinavia, Europe, the Mediterranean area and many parts of Britain. Fresh specimens contained as much paralysis virus as there is in bees killed by it in laboratory tests. Similar particles have been extracted by other workers from paralysed bees in the Ukraine, where Aleksenko and Kolomiets (1967) claim to have cultured the virus in 10–11-day-old chicken embryos, France (Giauffret *et al.*, 1966a) and Canada (Lee & Furgala, 1965a). There is no evidence that there are host species other than honey-

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bees: *Bombus*, *Psithyrus* and *Galleria* species were unaffected when injected with doses of virus that were lethal for honeybees (Bailey, 1965a).

Viruses obtained from almost all the countries mentioned above have been compared at Rothamsted and seem serologically indistinguishable from local ones, but Reinganum (1968) observed ring-shaped particles in purified preparations from bees with paralysis in Australia, and he found more long particles in bee samples during June (winter) than during September. Some variation in virus strains may be indicated by this, and their virulence may well differ.

Recent surveys in Britain show that at least 70% of samples of crawling moribund bees or of live bees from colonies producing very many crawlers in nature were of bees suffering from paralysis (Bailey, 1967a). Moreover, some of these samples contained many bees infected with *Acarapis woodi*, a parasitic mite long alleged to cause crawling in bees. However, only the sick bees in one of these samples, which was of many live bees, contained much paralysis virus, whereas *A. woodi* was distributed equally among the sick and apparently healthy individuals. Thus paralysis virus, not *A. woodi*, was causing the crawling.

Notwithstanding the world-wide distribution of paralysis virus, the percentage of colonies that are severely attacked is small, probably not more than 1 or 2%. However, in Britain at least, inapparent infection is very common. Electron microscopy of extracts of bees and serological evidence has suggested that a few particles of paralysis virus occur commonly in seemingly healthy bees (Bailey *et al.*, 1963; Bailey, 1965a). Infectivity tests with extracts of dead bees collected from beneath normal colonies showed that each of about 30% of the individuals contained more than about 10^7 particles of chronic paralysis virus, whereas similar extracts of live bees from the colonies were not infective (Bailey, 1967a). More than 10% of the dead bees contained as much virus as bees killed by chronic paralysis in the laboratory. Very recently (Bailey, unpublished), infectivity and serological tests with extracts of live bees from apparently healthy colonies with no history of paralysis show that during autumn and early winter at least, most bees contain some chronic paralysis virus. This virus is localised, occurring mainly in the post-cerebral and thoracic glands—i.e. the salivary or labial glands—with an average of about 10^5 particles per bee. Hypopharyngeal glands of the same bees contained about 10^4 particles per bee, but the heads of some individuals contained up to 10^8 particles. It may well be, therefore, that a large proportion of the very many bees continually lost from 'normal' colonies die of paralysis, as do many of the comparatively few individuals found dead nearby. 'Good' colonies of today must be only stunted versions of what they would be, were they free from chronic paralysis virus.

Multiplication and spread of chronic paralysis virus. About half the number of particles of chronic paralysis virus in a paralytic bee are in its head (Bailey *et al.*, 1968) which is about 1/10 of the total body weight. Extracts of the brains of paralytic bees are very infective and serological tests indicate that each brain is likely to contain 10^{10} or more particles. However, the only particles yet seen in sections of brain tissue that resemble those of paralysis virus were seen also in sections of brains from healthy bees, and may have been micro-tubules or other components of normal nerve tissue (Bailey & Milne, 1969). Lee and Furgala (1965a) saw similar particles in sections of the nerve ganglia of the thoraces and abdomens of paralysed bees but not in the ganglia of healthy bees. Whether these particles seen in nervous tissue were of chronic paralysis virus remains to be proved, but the infectivity of brain extracts and the symptoms of infection make it probable that the virus multiplies in nerve tissue. Giauffret *et al.* (1967) found many

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basophilic granules in the cytoplasm of the cells of the thoracic ganglia of paralytic bees, whereas the ganglia of uninfected bees contained none. These granules closely resemble those in the cytoplasm of the hind-gut of paralysed bees (Morison, 1936) and contained much nucleic acid of the ribose type.

The spread of paralysis between bees in nature has not been explained. About 10^{11} particles of chronic paralysis virus have been found in the 30 mg or so of liquid distending the honey-sac of the bloated paralytic bees found in nature (Bailey, 1970). Presumably the virus is secreted into the honey-sac from the salivary and possibly the hypopharyngeal glands, where it occurs even in healthy bees on some occasions (Bailey, unpublished), and one of the bloated paralytic bees would seem able to pass several lethal doses of virus in food to a few healthy individuals, according to the LD 50 found by laboratory tests. However, in other tests, bees injected with chronic paralysis virus failed to cause paralysis in healthy bees they fed entirely with food into which they had secreted the virus. Also, it was shown that virus passing into the faeces of paralysed bees soon lost infectivity, that virus accumulating in various tissues of bees fed sub-lethal doses quickly decreased after a few days and that colonies sprayed with virus suspensions suffered trivial and very transient losses of bees (Bailey, 1965a). Burnside (1933) observed that a few healthy bees became paralysed when placed in colonies with severe paralysis, but failed to transmit the disease by putting food from these colonies into healthy ones.

There is much circumstantial evidence indicating that susceptibility to paralysis is closely limited by inherited, possibly matroclinous, factors (Bailey, 1967a). Nevertheless, observations at Rothamsted for several years on colonies headed by queens bred from colonies with severe paralysis show that the onset of disease in them is unpredictable. Significantly more of these colonies have been severely weakened by paralysis than have colonies headed by normal queens but, at any one time, most remained apparently healthy even when kept in the same small area with the few that were severely diseased. Moreover, their bees have proved no more susceptible to artificial infection than bees from other colonies; also, although severely paralytic colonies have recovered when their queens have been replaced with queens from elsewhere, others have recovered spontaneously. One of the recovered colonies relapsed, severely affected and with the same marked queen, after seeming normal for a year (Bailey, 1967b, 1968b, 1969b). Environmental factors were possibly playing a part as they seem to have done when strains of bee susceptible to paralysis showed more disease when kept in uncultivated 'forest' regions in Germany than elsewhere (Drescher, 1964; Bailey, 1967a). Temperature may be important. Chronic paralysis virus multiplies more in bees at 30°C than at 35°C, yet it kills bees quicker at 35°C (Bailey & Milne, 1969). To some extent this reflects events in nature when much virus accumulates in live apparently healthy bees during autumn and winter and severe disease seems to occur mostly during summer, but it does not offer a ready explanation of the sudden and erratic nature of severe attacks. Perhaps extraneous toxins are involved. Maurizio (1945), for example, considered that bees apparently suffering from 'Waldtrachtkrankheit' and 'Maikrankheit', when they contain much chronic paralysis virus (Bailey, 1965a), sometimes had been poisoned with nectar containing glucosides such as saponin. Maurizio found these materials caused paralysis-like symptoms when fed to caged bees, and saponin increases the susceptibility of some cells to virus infection (Way, 1969), possibly by increasing their permeability. However, when bees known to be inapparently infected with chronic paralysis virus were fed toxic concentrations of saponin and other glucosides, the virus did not multiply (Bailey, unpublished). A likely possibility remaining is that susceptibility is not matroclinous and, because the sperm of the several individual drones that usually mate with one queen do

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not become entirely mixed within the spermatheca (Taber, 1955), a queen occasionally produces a flush of susceptible workers when using sperm mostly from a susceptible drone. This could explain the irregular occurrence of paralysis and the spontaneous recovery of a colony with the same queen.

All three castes of the honeybee are susceptible in nature to paralysis, seemingly at any age, and infected queens seem not to transmit the disease to their offspring. For example, some queens reared from severely paralysed colonies at Rothamsted have been found with paralysis only a day or so after they emerged from their cells, whereas others have mated successfully, laid many eggs, from which more apparently healthy queens and workers were reared, and have then died of paralysis. Extracts of the heads of the paralysed queens contained as much chronic paralysis virus as extracts of heads of paralysed worker bees and of paralysed mature drones. Young, moribund workers and drones, most probably less than 24 hours old, and even immature worker and drone pupae, found beneath paralytic colonies have contained as much virus as paralysed mature adults (Bailey, 1969b).

The hereditable factors causing susceptibility are probably recessive, otherwise queens that transmit them would soon be killed by paralysis. Drones, however, are haploid, so those carrying the factors would presumably be very vulnerable to infection. This seems an important mechanism selecting against the transmission of harmful genes and may well account for the rarity of colonies that are very susceptible to paralysis and to other disorders that are closely limited by genetic factors. Several years of observation on paralytic colonies at Rothamsted have produced no evidence that proportionately very many more drones die of paralysis than workers, but many may become infected, die and disappear while they are larvae. Larvae must become infected, otherwise the virus could not multiply, as it does, in pupae, although many attempts to infect worker larvae artificially in paralytic colonies, and so cause their deaths as pupae or adults, have failed. In fact, almost all of very many adults obtained by incubating pupae from paralysis colonies have been healthy. On one occasion, however, about half of about 100 newly emerged bees that had been left for a few hours on their comb became paralysed after a few days in cages, whereas further bees, caged as soon as they emerged from the same comb, remained healthy (Bailey, 1969b). This suggests that bees can become infected from the comb, and recently (Bailey, unpublished) infective chronic paralysis virus was found in pollen collected in the field by bees and removed from them before they could deposit it in their combs. The bees probably secrete the virus into the liquid they add to the pollen they collect. They probably infect larvae similarly, perhaps more efficiently than can be done artificially. Nevertheless, the spread and rapid multiplication of paralysis virus in nature seems very fickle. As other pathogens of bees, it seems to need several coincident factors before it causes much harm.

Retrospect. With our present knowledge of paralysis in mind it is interesting to consider some past accounts of adult bee diseases. One hundred and more years ago, but especially about 1905 when the so-called 'Isle of Wight disease' was alleged to have spread quickly throughout Britain and destroyed most of the bees, many amateur accounts in various journals, together with a few professional reports (e.g. Imms, 1907), described symptoms that match those of paralysis today. Although the allegations, often made then and subsequently, of a single infectious disease spreading rapidly throughout Britain, were never substantiated (Bailey, 1963), there is no doubt that disease quickly spread through some colonies of bees, as paralysis sometimes does today. The sight is impressive and soon trains the eye to notice far less severe examples. The virulence of paralysis virus

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when it multiplies, and the speed with which it can ruin a colony, contrasts especially with the nature of *Acarapis woodi*, which is popularly believed to have caused very severe and swift epidemics, but which can produce only five or six offspring per female and has a life cycle in its symptomless host of about 14 days. During this period, when *A. woodi* can multiply very little, even when circumstances for it are most advantageous, paralysis virus can multiply by many millions and almost destroy a large colony.

Strains of bees very susceptible to paralysis but free from virus may sometimes survive and multiply. Alternatively, and perhaps more probable, strains of bee may arise that are very susceptible to some strains of paralysis virus from elsewhere. In either event, spectacular losses can be expected when exotic virus strains are introduced. Local incidents of this kind seem to occur today when beekeepers propagate certain bee strains for various reasons and sometimes inadvertently select strains specially susceptible to paralysis (Bailey, 1967a). To replace them is a simple remedy when most other bee strains are resistant, and attempts made by beekeepers in these circumstances to find strains insusceptible to paralysis would soon succeed without any knowledge of the pathogen. However, the losses of bees in the past and the search for resistant strains by beekeepers are of unknown extent: the few records of losses suggest they were much exaggerated in most accounts (Bailey, 1963). Not very long afterwards, bees with the same symptoms were found to contain Morison's cell inclusions (Morison, 1936; Lotmar, 1940), which indicates that they were severely infected with chronic paralysis virus as we know it today, because the inclusions are specifically associated with chronic paralysis (Bailey, 1965a). There seem to be very good reasons, therefore, for suspecting that many of the colonies with crawling bees diagnosed in the past as suffering from the 'Isle of Wight', 'Nosema', Acarine' or 'Amoeba diseases' were really suffering from paralysis.

No other parasite of bees has been shown to cause such a severe and quickly fatal disease of the individual in which it multiplies, to be so constantly lethal to bees in nature, and to be so widespread as chronic bee-paralysis virus. Ironically it has attracted the least attention but it would presumably have had greater priority in research on bees long ago had it been as easy to detect as the well-known, large parasites of bees.

Sacbrood

White (1913, 1917), in the U.S.A., first described sacbrood clearly. He observed that larvae with the disease fail to shed their final skin about two days after they are sealed in their cells. The skin becomes a transparent sac, accumulating unusually much ecdysial fluid around the pupal integument. The larva then dies within a day or so and soon dries to form a flat brown scale in its cell, unless adult bees detect and eject it. White caused severe outbreaks of sacbrood by feeding bee colonies with sucrose syrup containing bacteria-free filtrates of diseased larvae. These larvae lost their infectivity about three weeks after they died.

Sacbrood virus. Steinhaus (1949) saw spherical particles about 60 nm across in extracts of larvae with sacbrood and Brčák *et al.* (1963) found isometric particles about 30 nm across, whereas they found no particles in extracts of healthy larvae. They made no tests to show that these particles would cause sacbrood. Bailey, Gibbs and Woods (1964), independently of Brčák *et al.*, also found isometric particles 30 nm in diameter and showed that purified preparations of them caused sacbrood when fed to honeybee larvae. Two-day-old larvae are the most susceptible and the median lethal dose for them by mouth is between 10^7 and 10^8 particles. About 10^{13} particles can be extracted from one larva

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with sacbrood (Bailey, 1969a). The nucleic acid of sacbrood virus is of the ribose type (Lee and Furgala, 1965).

Occurrence of sacbrood. Sacbrood was once thought to be rare, at least in Britain. Tarr (1937) thought most disease resembling sacbrood was a non-infectious hereditary fault—'addled brood'—because he failed to spread it by placing combs containing many diseased larvae in healthy colonies. However, as sacbrood does not spread readily this way (Hitchcock, 1966), and as the photographs shown by Tarr clearly resemble those of larvae known to have sacbrood (Bailey, 1967a), he was probably dealing with this disease.

Recent surveys show that over 80% of diseased honeybee larvae containing no visible organisms from England and Wales have sacbrood and that during summer 10 to 30% of apparently normal colonies, within about 20 miles of Harpenden, contain a few larvae with sacbrood (Bailey, 1967a). A signicantly greater proportion ($P = 0{\cdot}001$) of colonies of an imported strain of bees had sacbrood than local strains. Severe outbreaks occur during spring (White, 1917), but recent tests show that up to 6% of larvae from apparently healthy colonies in August have sacbrood (Bailey, unpublished). These tests were done by removing brood combs from their colony, without adhering bees, when individually identified larvae in them had just been sealed in their cells, and incubating them at 35°C for four days. Extracts of larvae that failed to pupate were then tested serologically for sacbrood virus. The incidence of sacbrood in a form severe enough to be easily diagnosed has now surpassed that of European foulbrood (Ministry of Agriculture, Fisheries and Food, 1969) and as both diseases are most severe during spring and early summer, it is not surprising that they sometimes occur together in the same colony (Bailey & Locher, 1967). The virus found in larvae with European foulbrood in France and thought by Giauffret *et al.* (1966b) to be a likely cause of this disease was, in fact, sacbrood virus (Bailey, 1969b).

Multiplication and spread of sacbrood virus. The ecdysial fluid in the sac that surrounds the dying larvae is rich in sacbrood virus but little is known of where the virus multiplies within the body of infected larvae. Lee and Furgala (1967a) saw particles, sometimes in crystalline array, in the cytoplasm of fat, muscle and tracheal-end cells 48 and 72 hours after 12–36 hour old larvae had been kept in the laboratory on food rich in virus. However, most of these larvae were classified as 'sick' or dead after 72 hours, at an age when they would still have been unsealed in the colony, so they were atypical of sacbrood larvae in nature, perhaps because they had ingested overwhelming amounts of virus. Fyg (1962) considered that infection upsets the production of moulting and juvenile hormones because analagous symptoms to those of sacbrood can be caused by ligatures that prevent the secretions of the brain and corpora allata from diffusing into most parts of the body of healthy larvae. Therefore, sacbrood virus may typically multiply in and derange these parts of the nervous system. The neurotropism of the virus was recently demonstrated by results of infectivity and serological tests showing that sacbrood virus multiplies in the brains of drones when it is injected into their haemolymph (Bailey, 1970).

White (1917) showed that one larva killed by sacbrood could infect about 3000 others when crushed in sugar solution and fed to the adult bees of a colony. Nevertheless, in natural circumstances, sacbrood usually disappears spontaneously during summer, and does not spread much even when combs containing many diseased larvae are placed in colonies (Hitchcock, 1966). In spite of this slight ability to spread during summer, of the rapid loss of infectivity of sacbrood virus in dead larvae, and of the absence of

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larvae during winter, sacbrood persists from year to year. A probable way it does so is by multiplying in adult bees. Bees of any age become infected when injected with about 10^3 particles and individuals younger than about eight days become infected when they ingest 10^8 particles of sacbrood virus (Bailey, 1969a). They show no symptoms, but much virus accumulates in their hypopharyngeal glands and, as they feed larvae with secretions —'royal jelly'—of these glands, they seem a probable source of infection. The youngest bees are not only the most susceptible to infection by ingesting sacbrood virus, but are also the ones most likely to ingest much in nature because they clean honeycomb cells vigorously on their first day of life (Lindauer, 1952; Sakagami, 1953). They detect and remove most sacbrood larvae within a day or two after the larvae die, when the virus is still infective, and they probably ingest ecdysial fluid when this is released from sacs that are ruptured in the removal process. The virus from less than 0·1 mg of a larva freshly killed by sacbrood is sufficient when ingested to infect one of these bees, and much sacbrood virus collects in their hypopharyngeal glands within two days after they ingest an infective dose (Bailey, unpublished). However, although infected adults show no symptoms, they eat little or no pollen after infection, so bees that are infected when they are the youngest and most susceptible are the least likely to eat pollen (Bailey, 1969a). They will, therefore, secrete the least royal jelly and so presumably will not feed many larvae. Moreover, their lack of protein reserves shortens their life and makes them least likely to survive the winter. Further, adults seem unable to infect each other with sacbrood virus when they exchange food. Probably only a comparatively few adults that have already eaten pollen and that then ingest sacbrood virus before they become immune are able to transmit virus to larvae. There seem to be many factors, therefore, that combine to prevent the rapid spread of sacbrood.

Although adult bees are probably the reservoir of sacbrood virus, no direct evidence has been obtained that they transmit virus they contain to larvae. The successful spread of sacbrood by adults fed on suspensions of sacbrood virus in sucrose solution is equivocal evidence because larvae may then be infected with virus carried mechanically by nurse bees. Small colonies composed entirely of worker bees injected with sacbrood virus reared only healthy larvae (Bailey, 1970) but the behaviour of the injected bees seemed abnormal and the very few larvae successfully reared in their colonies may have been fed by comparatively few bees in which virus had failed to multiply. Infection of adult bees in nature may well have more subtle effects than by injection.

Except for alternative host species, which seem improbable, the only other obvious way that sacbrood virus might be transmitted is through the queen, but many attempts to show this at Rothamsted have failed (Bailey, 1968b, 1970). The virus was injected into laying queens or fed to young individuals, which successfully mated and produced larvae. None of the queens transmitted sacbrood, although infectivity and serological tests with extracts of their heads showed that sacbrood virus had multiplied in them.

Drones, as workers, are most susceptible to infection by mouth when young and become immune to infection this way when they are about seven days old. However, the fact that sacbrood virus can multiply in drones is probably of no epidemiological significance, because it is improbable they will secrete virus from their vestigial salivary glands, and their chances of ingesting an infective dose in nature are small because they do not clean combs. None of 30 drones from a colony with severe sacbrood was infected (Bailey, unpublished). None of this present information about the multiplication and spread of sacbrood virus helps to explain why severe outbreaks usually occur only during spring and early summer, but the proportion of susceptible young adults and larvae may then be greatest because colonies are growing fastest.

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Acute paralysis

Acute paralysis was discovered as a laboratory phenomenon during work on chronic paralysis virus (Bailey, Gibbs & Woods, 1963). When 1 μl of bacteria-free, concentrated extracts of whole, apparently healthy, bees—e.g. ten bees extracted in 1 ml water—were injected into similar bees, most of these became flightless after about five or six days at 30°C, and then died within about a day. By contrast, bees injected with chronic paralysis virus remain flightless and trembly for a few days at 30°C before they die. The two kinds of paralysis are most easily differentiated when infected bees are kept also at 35°C. Those with chronic paralysis then die a little sooner than at 30°C, whereas those with acute paralysis, especially when injected with terminally infective dilutions, continue apparently normal for many days, some living as long as uninjected bees. When concentrated extracts of chronically paralysed bees are injected into apparently healthy bees, chronic paralysis virus multiplies, but after several serial passages of similarly concentrated extracts of the resulting paralysed bees, acute paralysis usually prevails.

Acute paralysis virus. Bailey, Gibbs and Woods (1963) extracted acute paralysis virus by grinding acutely paralysed bees in water + carbon tetrachloride, clarifying the extract at 8000 g for 10 minutes and then sedimenting the virus at 75 000 g for 2 hours. Infective virus can also be precipitated from clarified extracts by adding 1½ volumes of ethanol. It maintains infectivity for years in acutely paralysed bees preserved at −20°C. Acute paralysis virus has isometric particles about 30 nm in diameter which separate into two fractions with sedimentation rates ($S_{20,w}$) of 160 and 80, corresponding to particles that appear 'full' and 'empty' respectively when negatively stained with neutralised phosphotungstic acid and examined with the electron microscope. The particles closely resemble those of sacbrood virus but they are serologically distinct, and sacbrood virus kills only larvae whereas acute paralysis virus kills only adult bees (Bailey *et al.*, 1964). About 10^{12} particles, mostly full, can be extracted from one acutely paralysed bee; about 10^2 cause paralysis when injected into the haemolymph but about 10^{11} are needed to cause paralysis when ingested by a bee.

Occurrence. Acute paralysis virus has been detected in all of many samples of bees in Britain, by injecting apparently healthy individuals with concentrated extracts of similar bees from the same source. Similarly bees from N. America and Italy also contained acute paralysis virus (Bailey, 1965b) but bees from Asia and Australia did not (Bailey, 1964, 1967b). Several *Bombus* species in Britain are susceptible to acute paralysis virus and resemble British honeybees in being inapparently infected by it in nature, but *Vespula*, *Galleria*, *Achroia*, *Tenebrio* and *Blatta* species are insusceptible (Bailey and Gibbs, 1964).

Different colonies of bees differ greatly in the percentages of infected individuals (Bailey & Gibbs, 1964). Although the virus is widespread, bees suffering from acute paralysis have not been diagnosed in nature, but the very transitory symptoms of the disease would not make diagnosis easy in the field.

Results of several recent tests (Bailey, unpublished) show that most bees injected with concentrated extracts of live bees from winter clusters at Rothamsted do not become acutely paralysed, even after three serial passages of extracts in winter bees, whereas most test bees from the same source and at the same time were killed by acute paralysis virus when injected with similar extracts of apparently healthy bees that had been collected during summer.

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Multiplication and spread of acute paralysis virus. There are probably not more than about 10^5 particles of acute paralysis virus per apparently healthy bee, and most seem to be in the abdomen, perhaps limited to the intestine (Bailey & Gibbs, 1964). However, bees showing symptoms have much virus in several different tissues, such as the cytoplasm of the fat-body cells (Furgala & Lee, 1966), the brain and especially the hypopharyngeal glands (Bailey & Milne, 1969). Virus accumulates in various tissues of bees, shortly after these are fed sub-lethal doses, but then slowly decreases without causing apparent harm. It becomes systemic and lethal probably only when some particles enter the haemolymph, because antiserum, prepared in rabbits against the virus and injected into the haemolymph protects bees equally against infection by mouth or by injection (Bailey & Gibbs, 1964).

Acute paralysis virus has recently been detected by infectivity and serological tests in pollen freshly gathered by bees (Bailey, unpublished). There were at least 10^5 particles per gram. Although other sources of the virus have not been excluded, bees probably secrete it from their glands, as they do chronic paralysis virus, into the fluid they add to pollen as they collect it. Thus acute paralysis virus seems to multiply and spread most during summer, probably from gland secretions because bees injected with lethal doses of virus transmit it in the food they pass to uninfected individuals in cages (Bailey & Gibbs, 1964). There may be a relationship between the summer multiplication of acute paralysis virus and temperature, because more than three times as much virus can accumulate in living bees at 35°C, which is the usual temperature within the summer cluster, than in bees killed by acute paralysis at 30°C (Bailey & Milne, 1969). These effects of temperature are the converse of those on chronic paralysis virus, which multiplies more at 30°C than at 35°C but kills bees sooner at 35°C. However, an important point of similarity between both viruses is that the severity of their effect is not simply related to the amount that they multiply.

In view of the physical similarities between the particles of acute paralysis and sacbrood viruses and the fact that both multiply in adult bees, their effects, especially on drones, are unexpectedly different. Acute paralysis kills drones at 30°C within a week of injecting the virus and the brain contains about 10^{11} particles, whereas sacbrood virus, which also multiplies in the brain and other tissues at least as much as does acute paralysis virus, causes no symptoms at any temperature and shortens the life of a drone by only a few days (Bailey, 1970).

Some evidence (Bailey & Gibbs, 1964) seemed to indicate that acute bee-paralysis virus could be activated by injecting adult bees with either foreign proteins or concentrated preparations of sacbrood virus (Bailey, 1967c). Later, however, some preparations of sacbrood virus failed repeatedly to cause acute paralysis whereas other preparations always did (Bailey, 1969b), so it seems that sacbrood preparations are frequently contaminated with acute paralysis virus. Similar evidence of contamination was obtained recently when one preparation of sacbrood virus caused chronic paralysis when injected into adult bees (Bailey, unpublished). Possibly the particles seen by Lee and Furgala (1967b) in sections of the fat-body of apparently healthy bees they had injected with sacbrood virus were also particles of acute paralysis virus, especially as they had incubated their bees at 35°C, at which temperature bees infected with acute paralysis virus do not soon die.

As acute paralysis virus occurs commonly in apparently healthy bees, at least during summer, it is likely to contaminate their products and be transmitted when extracts of these are injected into adult individuals. However, transmission can usually be avoided by diluting the extracts, e.g. so that no more than about 10^5 of the extract of an adult

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or a larva is injected. Alternatively, the virus can be neutralised by mixing extracts, before they are injected, with antiserum to it prepared in rabbits.

Conclusions

As there are at least three viruses that can cause severe diseases of the honeybee but that commonly persist without causing symptoms, many similar viruses might be expected to occur in other insects, but very few have yet been found. The only good examples seem to be a virus of termites (Gibbs, Gay & Wetherly, 1970) and 'Sigma' virus of *Drosophila melanogaster* (Seecoff, 1968). The termite virus, moreover, has particles resembling those of acute bee-paralysis virus and kills its host when injected into the haemolymph. Sigma virus kills its inapparently infected host only when the insect is anaesthetised with CO_2, which is at least reminiscent of sacbrood virus causing effects similar to those of CO_2 in adult bees. The best known viruses that attack insects are their peculiar polyhedrosis and granulosis types, which are enclosed in large protein crystals, and the large iridescent types (Smith, 1967). There is some evidence of inapparent infections by some of the polyhedrosis viruses but none has consistently and unequivocably been shown to persist this way. Social insects, especially those with perennial colonies, would be very severely handicapped by host-specific parasites that invariably caused severe disease, so inapparent virus infections are perhaps most likely to evolve among them.

Honeybee viruses seem to have less in common with pathogenic viruses of other insects than with the very many viruses of other animals and plants. They resemble especially the arthropod-borne viruses of plants and animals, not only in being of similar size and in being unenclosed in protein crystals, but in multiplying as inapparent infections and accumulating in the salivary glands of adults. Sacbrood virus is especially striking in this respect, as it does not cause symptoms in adults when it multiplies greatly, even in the brain tissue. The declining concentration of chronic and acute paralysis viruses with time in various tissues of bees that have been fed sub-lethal doses of virus, resembles the behaviour of Semliki forest virus in *Aedes aegypti* (Mims *et al.*, 1966). This behaviour may also be analagous to that of some plant viruses, which, although persistent in vectors that feed for long on infected plants, become established only temporarily in vectors that feed briefly. This phenomenon has been advanced as evidence against the multiplication of such plant viruses in their vectors (Black, 1959). Whether sub-lethal doses of the bee-paralysis viruses multiply or simply accumulate temporarily in their host is uncertain, but the persistence of the viruses through generations of seemingly healthy individuals, with no known alternative hosts, makes it probable they usually multiply and spread as inapparent infections. Only rarely, when the unknown mechanism that limits their spread within the body of a bee is overwhelmed or bypassed, do they attack vital centres. It might be supposed that the gut of adult bees absorbs all of a sub-lethal dose of paralysis virus whereas some of a lethal dose passes through to the haemolymph and becomes systemic, as arboviruses do in mosquitoes (Chamberlain, 1968). This supposition is supported by the ability of antiserum injected into the haemolymph of bees to protect them against lethal oral doses of virus. However, sub-lethal doses of chronic and acute paralysis viruses become temporarily established in several tissues additional to the gut (Bailey & Gibbs, 1964; Bailey, 1965a) so the infective process may not be very clearly demarcated between tissues.

The bee viruses probably cause their severe pathological effects by multiplying in nervous tissues, but they must affect these in different ways. This is suggested by the converse effects of changes of temperature on the multiplication of chronic and acute

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paralysis viruses and on the speed at which they kill when infected bees are incubated at 35° and 30°C, and by sacbrood virus multiplying but causing no overt symptoms in adults at any temperature. These contrasting responses of infections by different viruses in the same host to the same environmental conditions suggest that precise specific factors control the multiplication of each virus. They do not support the concept of 'stress', in its usual non-specific sense, as an activator of virus diseases of insects (Smith, 1967). Nor does the appearance and disappearance of paralysis on different occasions in different colonies within the same small area during summer, when most colonies are flourishing. Additional unknown factors are obviously required for chronic paralysis virus, and probably sacbrood virus, to spread and cause severe disease, but they are probably specific, as are the known factors required for most other pathogens of bees to multiply and spread (Bailey, 1968a). To label them all as stress is retrograde, especially as there are very many circumstances that warrant the same description but do not influence, or sometimes even inhibit, the multiplication of parasites.

As most other parasites of bees, sacbrood virus multiplies freely within individuals it infects and its spread within the population is controlled by various activities of bees, including the frequent replacement of susceptible individuals during summer and their lack during winter. The proportion of susceptible individuals increases or decreases seasonally, which probably causes disease outbreaks or spontaneous recovery, and hereditary factors seem of secondary influence. By contrast with this mainly dynamic process of disease control, the multiplication of the paralysis viruses is usually checked within each of the very many infected individuals by innate resistance factors.

It might be easy to select strains of bees containing substantially less chronic paralysis virus than average by rearing queens from colonies that lose fewest workers from paralysis or that contain least virus. In this way it may be possible quickly to produce much more vigorous colonies than those of today. Virus-free colonies may be attainable by some non-genetical method but to protect them against reinfection from surrounding inapparently infected bees seems a formidable task.

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Management of Honeybee Colonies for Crop Pollination

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Butler and Simpson (1953) reviewed fundamental work done at Rothamsted on the foraging behaviour of honeybees, especially in relation to nectar secretion. More recent studies of this type are discussed by Free (1970a). This review deals with the use of honeybee colonies to increase seed or fruit production.

Pollination requirements of crops

The extent to which insect pollination increases the yield of a crop differs greatly with different crops. A standard method of determining whether a crop benefits from insect visits is to compare the yields of plants that are : (a) covered by nylon screen cages containing honeybee colonies, (b) covered by cages to exclude insects and (c) not caged.

Insect pollination of some species produces either no increase in yield or such a small one as to be difficult to demonstrate. Thus, the average yield of *Brassica napus*, caged with bees, not caged, and caged without bees was respectively 806, 729 and 714 seeds per plant with a mean weight of 2·85, 2·98 and 3·05 g per 1000 seeds (Free & Nuttall, 1968a). Similarly, *Brassica juncea* produced a mean of 2727 seeds per plant when caged with bees, 2403 when not caged and 2302 when caged without bees (Free & Spencer-Booth, 1963a), and *Phaseolus vulgaris* plants produced a mean of 45 seeds of 0·64 g mean weight when caged with bees and 40 seeds of 0·61 g mean weight when caged without bees (Free, 1966a).

Other species yield substantially more with than without insect pollination. For example, *Brassica alba* produced a mean of 486 seeds per plant when caged with bees and 213 seeds per plant caged without bees (Free & Spencer-Booth, 1963a). *Vicia faba* also produced more seeds per plant when caged with bees than when caged without bees (broad beans, 23·9 : 15·1 respectively; field beans, 18·1 : 14·5 respectively; Free, 1966b). More *Fragaria x ananassa* flowers visited by bees than isolated from bees set fruit (65·5 : 55·7% respectively, Free, 1968a).

Some species cannot produce even a moderate crop without insect pollination; thus, *Phaseolus multiflorus* produced only 30 seeds per plant when isolated from bees but 206 seeds per plant when caged with bees (Free, 1966a; Free & Racey, 1968a) and *Helianthus annuus* heads isolated from insects set little or no seed (Free & Simpson, 1964).

Some species (e.g. *Ribes nigrum*, Free, 1968b) yield similarly whether cross-pollinated or self-pollinated, but others set fruit or seed only when they receive pollen from another clone or variety, and still others yield more when cross-pollinated. Thus, cross-pollination between heads of different plants of *Helianthus annuus* produced more seed than pollination between different heads of the same plant (45 and 24% set respectively) (Free & Simpson, 1964). Many varieties of *Prunus* and *Pyrus* are well known as needing cross-pollination. Despite suggestions to the contrary, it has been confirmed that insects are mainly responsible for transferring pollen from pollinizer to main variety trees and wind plays little or no part in doing so (Free, 1964a).

The pollinating efficiency per bee visit is usually less for species or varieties needing

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cross-pollination than for those that set well with self-pollination, because on many visits the insects do not carry compatible pollen. Thus, visits by single bees set fruit on only 11% of *Pyrus malus* flowers, var. 'Cox', which need cross-pollination, whereas they set 57% of 'James Grieve', which often sets well when self-pollinated (Free, 1966c). Many bee visits to *Trifolium pratense* flowers, which are almost completely self-sterile, also fail to cross-pollinate and set seed (Free, 1965a).

Insect pollination sometimes has advantages in addition to increased seed or fruit yield. Thus, bee visits not only increase the set of *Fragaria x ananassa* flowers but also produce larger berries and give fewer malformed berries (Free, 1968a). Pollination by bees can also produce an earlier and more uniform harvest. For example, although Riedel and Wort (1960) found no effect of bees on total yield of *Vicia faba* (field beans), the plants with bees produced more pods from flowers on low than on high nodes. Free (1966b) also found this effect with broad beans. Bees both increased the number of pods produced by *Phaseolus multiflorus* and the proportion of early maturing ones (Free, 1966a).

Although experiments with caged honeybees are useful in determining the pollination requirements of crops, the results sometimes underestimate probable yields when colonies are taken to a field of the crop, because caged plants often yield less than uncaged ones. This is partly because colonies confined in cages become increasingly inactive and forage less, so plants in the open plots are visited more freely by pollinating insects. This inertia can be avoided to some extent by confining the bees in the cages on alternate days only (Butler & Haigh, 1956), or by allowing most of the foragers of a colony continuous free range while diverting a few into the cages at intervals throughout the day (Free, 1966a). However, because bees do not cleanse their bodies thoroughly of pollen between foraging trips (Free & Durrant, 1966), the latter method is inadvisable when caged bees are being used for controlled plant breeding. Indeed, part of the reason for plants in the open plots yielding more may be that they are not restricted to pollen from one, or a few, sources.

Excluding bees from plants without otherwise altering the environment is impossible and the cages themselves can produce large differences in plant growth and yield. Diminished light in cages makes potential yield smaller and diminishes the benefit of insect pollination (e.g. *Vicia faba*, Free, 1966b). Prolonged flowering in cages without bees probably indicates that the plants concerned could bear more seed than that already set. Caging must also make wind pollination less likely.

However, cage experiments may also overestimate the yield response likely in the open. Sometimes this may be because caged honeybees can only visit the, possibly relatively unattractive, flowers in the cages, whereas those outside can choose any more attractive ones that are present. Also, honeybee visits may sometimes be more efficient in the cages than in the open field. Honeybees in the field often obtain nectar through holes bitten by 'robber' bumblebees (e.g. *Bombus lucorum* and *B. terrestris*) in the bases of flowers with long corolla tubes (e.g. *Trifolium pratense*, *Vicia faba*) and fail to pollinate the flowers. They cannot make such holes themselves, so in cages they must enter the flowers and thereby pollinate them. Although most honeybees fail to pollinate *Phaseolus multiflorus* flowers in the field (Free, 1968c), they are efficient pollinators in a glasshouse and produce an earlier and more profitable crop (Free & Racey, 1968a).

One method to avoid the difficulties associated with caging plants is to bag individual flowers or flower heads, except during periods of observation when any bee visits are recorded, and to determine later whether these visits have increased the set (Free, 1965a, 1966c). However, this can be done only with flowers that are easily bagged without damage and, although it shows the effect of insect pollination on the set of individual

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flowers or flower heads, it does not give information on the effect of increased pollination on the yield of the plant as a whole.

Whatever method is used, some flowers should be hand-pollinated (e.g. Free, 1964a, 1966c) to know what is the maximum set possible in the prevailing conditions. Hand-pollination of experimental plots in a sample of fields can be used to find whether inadequate pollination is a factor limiting yield (Butler *et al.*, 1956).

Although blowflies and bumblebees can sometimes be used to pollinate plants in glasshouses or cages (Free & Racey, 1968a), economic methods of using wild bees to pollinate field crops have yet to be developed, although some preliminary tests have given interesting results (see Free & Butler, 1959; Butler, 1965; Free & Williams, 1970a). At present the honeybee is the only pollinating insect that is readily obtainable in large numbers when required. However, taking honeybee colonies to crops will rarely give such large increases in yield as exist between caged and uncaged plots because there are often many insects, including other honeybees, already visiting the flowers. The need for a grower to hire honeybee colonies depends on many factors including the attractiveness of the crop to honeybees and their ability to pollinate it, the number of other insects usually present, and the probable increase in yield from insect pollination. All these factors will differ with different species of crop. For example, Free (1968d) found that honeybees were usually more numerous than bumblebees on *Rubus idaeus*, although their numbers fluctuated more, whereas bumblebees were the more abundant on *Ribes nigrum*. Although many types of insects, especially Diptera, visited *Fragaria x ananassa* flowers, honeybees were scarce and tended to be limited to good weather. Hence, unless a *F. x ananassa* plantation is large, it might not be economically worthwhile for a grower to hire honeybee colonies. However, honeybee colonies can profitably be employed in glasshouses to obviate the need for laborious hand-pollination. If blowflies prove to be as efficient pollinators as honeybees in glasshouses, they would perhaps be even more convenient and economical.

Because of their structure and behaviour, bees are better pollinators than other flower-visiting insects, which often fail to transfer pollen. Correlations have been obtained between honeybee abundance on different parts of a crop and the yield obtained (e.g. Free, 1962a). Even when honeybees are much fewer than all other insects, they may be responsible for most of the pollination (Lewis & Smith, unpublished).

It is commonly supposed that the number of wild pollinating insects has been greatly diminished by changes in farming practice, including increased use of insecticides and herbicides. Partly because of this supposition the demand for honeybee colonies for pollination has increased and will probably continue to increase as the value of bees becomes more widely appreciated. However, the number of honeybee colonies in England and Wales has decreased greatly; by about 30% during the last decade alone. Hence, it is important that the remaining colonies should be used as efficiently as possible and protected from insecticides. It is perhaps significant that, despite frequent spraying of orchards, which growers recognise need insect pollination, bees are rarely poisoned in them, and most bee poisonings are attributable to spraying of *Vicia faba* (field beans) (Needham & Stevenson, 1966; Needham *et al.*, 1966), where the need for bee pollination is neither so obvious nor so well appreciated.

Number of bees needed

Although small colonies are more useful for pollination than was previously suggested (Free & Preece, 1969), large colonies have greater foraging populations at all times and

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are to be preferred. Hence, it is sometimes advantageous to feed colonies supplementary protein and carbohydrate (e.g. Butler *et al.*, 1952; Spencer-Booth, 1960; Free & Spencer-Booth, 1961) to encourage their growth in time for the flowering of crops needing pollination.

It is difficult to advise on the number of colonies needed for a given area of crop. Any estimate must take into account the size of the colonies, the attractiveness of the crop, the density of flowers, the amount of nectar and pollen, the number of pollinating insects including honeybees already present, the behaviour of bees on the crop and, of course, whether the flowers need cross-pollination.

In parts of the world where it is dry, warm and sunny during the flowering of a crop, the seed and fruit set can be correlated with the number of bees foraging per unit area, so that growers in these places know whether to increase the bee population by importing further colonies (Free, 1970a). The weather in Britain, which often prevents foraging, or makes the flowers unattractive, for long periods, precludes such assessments, and it is usually necessary to provide enough colonies to ensure adequate pollination when pollination is possible during only a part of the flowering period. Such estimates (Free, 1966c, 1970a) suggest that recommendations of $2\frac{1}{2}$ colonies per hectare of well-planned orchard (e.g. Ministry of Agriculture, Fisheries and Food, 1962) are probably justified.

Wherever possible bees should be abundant soon after flowers open, because the viability of flowers of many species (e.g. *Trifolium pratense*, Free, 1965a) rapidly diminishes as they age.

Attempts to increase bee visitation to crops

Examining the pollen loads of successful foragers shows that very few honeybee colonies forage on anything like the maximum number of flower species visited by bees in their neighbourhood (Synge, 1947; Free, 1959). Colonies in the same location differ greatly in the number of flower species they visit, and some may visit twice as many as others. The differences between colonies usually show in species that provide only a small proportion of their total pollen requirements, but sometimes a colony will forage extensively on a species that neighbouring colonies rarely visit. However, the principal species on which bees forage tend to be visited to some extent by all colonies. Whereas these differences seem partly to depend on the preferences of bees for specific pollens, which exist even when the pollens are presented in glass dishes in the hive (Synge, 1947), they also depend on the previous foraging of the colony.

During a single foraging trip most bees (usually over 90%; see Free, 1963) visit only one species, but only about half the foragers remain constant to the original species for a week or more. The actual percentage that keeps constant differs in different conditions and with different colonies, but bees that collect the most common pollen tend to be the least likely to change, probably reflecting its greater attractiveness and abundance. Presumably changes from one species to another reflect changes in their qualities and the differences in specific constancy found in different experiments reflect differences in foraging conditions. However, when pollen is temporarily unobtainable from the species they are visiting, most bees stop foraging or collect nectar only, at least for a time, rather than collect pollen from another species. Hence, bees are reluctant, but not unable, to change species and this temporary fixation, together with adaptability over a longer period, seems to explain their rate of change (Free, 1963).

The behaviour of individual bees is reflected in the behaviour of the colony as a whole, and, although the amount of pollen of a given species that is collected by the colonies of

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a group often remains relatively constant over a short period, changes do occur. Thus, a colony that has collected only relatively small amounts of pollen from one species at an early stage of its flowering may eventually collect more of it than its neighbours, and, conversely, those that originally collected much of their pollen from one source may later collect only little from it (Free, 1959).

When colonies are taken to a crop before flowering has begun, most of the foragers become conditioned to visiting other flower species in the locality, and will not readily forsake them when the crop requiring pollination comes into flower. It has been found that the proportion of foragers visiting a crop can be greatly increased by not taking the colonies to it until it has begun to flower. Crops used in these experiments include *Vicia faba*, *Papaver somniferum*, *Prunus persica*, *Prunus avium*, *Pyrus malus*, *Lotus corniculatus*, *Medicago sativa*, *Trifolium pratense* and *Brassica nigra* (Free, 1959; Free *et al.*, 1960; Free, 1965b).

However, although colonies moved to a new site exploit a crop that has recently come into flower more than do colonies that were there previously, sometimes they continue to visit species they visited at the old site (Free, 1959; Free, 1963). The species to which a bee changes at a new site is also sometimes influenced by the species previously visited; thus, moved bees that had previously collected Cruciferous pollen, but not *Brassica alba* collected more *B. alba* pollen than bees that had collected other pollen. The actual amount of a given pollen that a colony collects after being moved is sometimes related to the amount collected previously. The odour of the food stores in a colony also plays a part in determining the species the foragers will visit, although a less important one than the previous experience of the foragers (Free, 1969). The interaction of these factors determines the extent to which a moved colony concentrates on the crop needing pollination.

A crop may be less attractive than others further away, and the proportion of bees from colonies that visit it sometimes then decreases rapidly (Free & Smith, 1961). The adaptability of bees to better forage (Ribbands, 1949; 1955) and their short foraging lives (Free & Spencer-Booth, 1959), probably explain this decrease. Delaying taking colonies to such crops until they are in flower, is relatively even more advantageous because it ensures that pollination will be considerable before its bee population greatly decreases.

A flower presents most of its pollen at a time of day characteristic of its species (Synge, 1947). Thus, *Taraxacum officinale* presents most of its pollen during the forenoon and *Pyrus malus* during the afternoon. When both are flowering in the same area, *T. officinale* is a severe competitor to *P. malus* for bee visits (Free, 1968e). It has been found that more bees become conditioned to collecting *P. malus* pollen when colonies are prevented from foraging until the afternoon of the day they are taken to a *P. malus* orchard than when they are allowed to forage early in the morning (Free & Nuttall, 1968b).

The same principle probably applied to other crops (e.g. *Pyrus communis*, *Prunus persica*, *Trifolium repens* and *Vicia faba*) that present their pollen mostly or exclusively in the afternoon. Delaying release of the bees until the afternoon might be especially useful in inducing them to visit *Vicia faba*, a species they are often reluctant to work (Free, 1964b) although they sometimes do so enthusiastically, presumably when there is no competition from other flowers (e.g. Free *et al.*, 1967).

Attempts to induce bees to visit certain crops by feeding them with sugar syrup in which flowers of these crops have been immersed have failed at Rothamsted (Butler and Simpson, 1953; Free, 1958). Attempts to increase pollination of *Vicia faba* and *Pyrus malus* by spraying these crops with sugar syrup have also been unsuccessful (Free, 1965b) and, although spraying increased the number of bees collecting the syrup, fewer collected

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nectar and pollen, partly because many were diverted to collect syrup and partly because the anthers were wet. In the *P. malus* orchard spraying syrup actually decreased set.

Although the amount and concentration (Butler, 1945) and the composition (Wykes, 1952; 1953) of nectar present, and the amount of pollen (Synge, 1947) may be largely responsible for the greater attractiveness of some species or varieties of flowers than others (see Free, 1970a), other factors may also be important. Thus, Synge (1947) found that *Trifolium repens* pollen was preferred to *Trifolium pratense* pollen when taken from the flowers and presented to the bees in equal quantities, presumably because it had a more attractive odour. Perhaps differences in the attractiveness of odours in the nectar or floral parts of different species may also be important in determining the extent to which they are visited. The Nasonov scent gland of the worker honeybee is in a fold between its 5th and 6th dorsal abdominal tergites. Bees collecting water (Free & Williams, 1970b) or a plentiful supply of nectar and syrup (Free & Racey, 1966) often open these glands, especially at sites without any visual or scent orientation marks (Free, 1968f). The odour produced attracts other bees (Free & Butler, 1955), including scout bees and searching bees, to the source and stimulates them to alight (Free, 1968f) thus resulting in increased exploitation of the crop. Indeed, an experiment by C. R. Ribbands and J. B. S. Haldane (Butler, 1955), designed to assess the accuracy of crop communication, showed that body odour played an unexpectedly large part in attracting recruits to the immediate vicinity of foragers. Nasonov gland odour consists of geraniol (about 97%) and both isomers of citral (about 3%), and a mixture of these is about as attractive to foraging bees as the Nasonov gland odour itself (Butler & Calam, 1969). Therefore, Nasonov gland odour on flowers would probably attract 'scout' bees to them, in addition to the recruits directed to the flowers by the dances of successful foragers. Hence, if the Nasonov gland odour or attractive floral odours could be synthesised and applied economically, they might be used to increase the number of bees visiting agricultural crops that need pollination.

Foraging areas of colonies and their distribution in a crop

The distance bees have to fly to reach a crop is another factor that determines its attractiveness. When Ribbands (1951) sited groups of colonies at the edges of crops in flower and 0·6 km and 1·2 km away from them at places where there was little or no other forage, the amount of honey stored in the colonies decreased with increasing distance from the crop. This effect was greater during poor foraging weather (when bees tend to confine their foraging near their hives (Butler *et al.*, 1943), and sometimes, under such conditions, colonies at the crop gained weight while those in the other groups lost it. Hence, taking colonies to a crop is important in determining the number of bees that forage. It is also important in shortening the time spent flying between crop and hive, and so increasing the proportion of time bees spend in actual foraging. Because pollen loads are usually collected quicker than nectar loads (Ribbands, 1953), a pollen-gatherer spends more of its foraging trip in travelling to and fro; hence shortening the distance between the hive and crop benefits pollen-gatherers more than nectar-gatherers.

The optimum foraging range of colonies should be considered when determining their distribution on a crop. Individual bees tend to select the most favourable forage they find near their hives, this is reflected in the foraging areas of their colonies, and needs considering in trying to ensure an even distribution of foraging bees on a crop. It is convenient for both grower and beekeeper to put colonies in as large groups as possible, but when groups are too far apart foraging bees are concentrated near their hives,

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especially during bad foraging weather, and there are few remote from them. An uneven distribution of foragers can be reflected in crop yield. When colonies in fruit orchards are put in small equidistant groups of four or five colonies, at the rate of 2½ colonies per hectare, the foraging area of adjacent groups overlaps enough to ensure a uniform distribution of foragers (Free & Spencer-Booth, 1963b). Foraging populations also decreased with distance from their hives on a field of *Brassica alba* (Free, 1970a) but the more advanced stage of flowering of one part of the crop also had a pronounced effect. The optimum size, for both grower and beekeeper, of the groups to be used will probably depend on the species of crop, and the many factors that may influence size and location of the foraging areas of colonies need further study. For example, Lewis and Smith (1969, and unpublished) found that more bees and other insects visited *Pyrus malus* in the shelter of large windbreaks than elsewhere in an orchard; whether this distribution reflected the greater amount of nectar and pollen in the shelter, or the effect of the shelter itself, remains uncertain.

In a glasshouse, bees also prefer to forage near their colonies, and with one colony the bees are more evenly distributed when it is near the centre of a glasshouse than at one end. With two colonies, it is best to place them near diagonally opposite corners of the house to counteract the tendency of bees to work along rather than across the rows (Free & Racey, 1966).

Foraging areas of individual bees and orchard planning

A bee does not travel far over a crop while foraging, and all its flower visits during a single foraging trip may be within an area of a few squares metres (e.g. *Vicia faba*, Free, 1962b; *Helianthus annuus*, Free, 1964c; *Rubus idaeus*, Free, 1968d). The size of the area over which a bee forages during a single trip depends on many factors including the distance the plants are apart, the number of flowers per plant, the stage of flowering, their nectar and pollen production, weather; also on the number of pollinating insects, because this affects the food supply and the likelihood of them disturbing each other. However, a foraging trip usually comprises visits to several individual plants, so ensuring that pollen is transferred between plants needing cross-pollination. The tendency of bees to visit only a few of the flowers that are open on a plant helps achieve this. Thus, on average, a bee visits about 22 florets per *Helianthus annuus* head (Free, 1964c), about 20% of the florets on a *Trifolium pratense* head (Free, 1965a) and about 13% of the open flowers on a *Fragaria x ananassa* plant (Free, 1968d).

However, when the plants are large (e.g. fruit trees and bushes) the spread of an individual bee's foraging may be a factor limiting cross-pollination. In fruit orchards of standard trees a bee visits an average of only about two trees per foraging trip and moves between trees are usually between adjacent ones. When the distance separating rows is greater than that separating trees within a row, the bees tend to move along rather than across the rows (Free, 1960). This suggested that main variety trees needing cross-pollination that were next to a pollinizer variety would be better pollinated than trees further away. Observations in orchards of *Pyrus malus*, *Pyrus communis*, *Prunus avium* and *Prunus domestica* confirmed this and showed that fruit set often decreased greatly as the distance between pollinizer and main variety trees increased (Free, 1962a; Free & Spencer-Booth, 1964a). Further, the sides of main variety trees facing pollinizer trees often had a greater fruit set, more seeds per fruit, and more carpels with seeds per fruit than the far sides. Parts of trees containing cut branches of a pollinizer variety set better than parts without such 'bouquets'. These differences not only reflect the short

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movements of the individual foragers but also indicate that, when a bee moves from a pollinizer to a main variety tree, it probably pollinates only the first few flowers it visits; presumably the compatible pollen on its body is soon either packed into its corbiculae or greatly diluted with main variety pollen. In some orchards bees were more abundant on the south than on the north sides of the trees; partly because of this, perhaps, the set was also sometimes greater on the south side. In an orchard of dwarf pyramid *Pyrus malus*, most bees visited flowers in only about 9 m of a continuous row during one foraging trip and few changed from one row to another (Free & Spencer-Booth, 1964b). Because of this, set was greater on rows adjacent to a pollinizer row than on rows further away (Free & Spencer-Booth, 1964a; Free, 1966c).

In many of the orchards studied the average set was less than that necessary to obtain a good commercial crop. Pollination could be increased either by increasing the foraging areas of the individual bees, or by arranging the planting of the orchards to take the sizes of the foraging areas of the bees into account. Increasing the number of colonies in an orchard, and hence competition between the bees, might seem likely to increase the distances bees travel, but there is no evidence that it does (Free, 1966d). Because it might lead to a greater proportion of the bees foraging elsewhere, it could be wasteful, and it seems preferable to allow for the limited foraging areas of bees when planting orchards. Grafting scions of pollinizer varieties on the main varieties, is one way of getting a maximum and even set on each main variety tree but it creates picking problems. Another is to surround main varieties by pollinizers (see Free, 1970a, for planting arrangements); the ratio of pollinizer to main variety trees must strike a balance between the amount of set required and the relative value of the fruit of the two types. To increase pollination in dwarf pyramid orchards, pollinizer trees should be at intervals of not more than 3 m and in the same rows as the trees of the main variety.

Although set is usually greatest nearest to pollinizer trees, usually a few flowers set fruit on trees that are distant from pollinizers, and many more do so than would be expected from the behaviour of bees during a single trip. However, a bee usually covers a larger area during consecutive trips than during a single trip. In an orchard of dwarf *Pyrus malus* trees the mean size of areas visited was 338 sq m after two days foraging and 1016 sq m after eight days foraging (Free and Spencer-Booth, 1964b), by when the bees had made many moves between the two varieties, 'Cox's Orange Pippin' and 'James Grieve', in the orchard. Observations in an orchard of standard *Pyrus malus* trees of five varieties (Cox's Orange Pippin, Sunset, Laxton's Fortune, Merton Worcester, Tydeman's Late Orange) arranged in discrete rows showed that, provided a variety retained or increased its attractiveness, most bees kept to it and even preferred it to a more attractive variety (Free, 1966d). Over five consecutive days bees visiting the varieties that were persistently or increasingly attractive (i.e. Laxton's Fortune and Sunset) had smaller foraging areas than those originally visiting varieties that became less attractive (i.e. Merton Worcester, Tydeman's Late Orange). The attractiveness of a variety was correlated with the abundance of its flowers and its stage of flowering, and, as a variety became less attractive, the bees visiting it moved to another and so increased their total foraging areas, although they did not necessarily have larger foraging areas during a single trip. The attractiveness of a late flowering variety was enhanced by its proximity to a variety the bees had been visiting.

While bees are in their hives between foraging trips they fail to clean their bodies completely of pollen, and enough remains viable to pollinate flowers during the next trip (Free & Durrant, 1966). Hence, because consecutive trips are not to exactly the same area, and sometimes embrace more than one variety, compatible pollen is distributed

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more widely than during a single trip. Bees probably move between different varieties most often when the varieties are equally attractive, have concurrent flowering periods, and the bees do not differentiate between them. To encourage cross-pollination during consecutive trips the varieties concerned should not be separated in discrete rows.

However, cross-pollination is possible even when individual bees remain constant to one variety from trip to trip because, although most of the pollen on the body of a bee leaving a hive belongs to one species there are usually some grains of a few other species (Free, 1966e). Probably this 'foreign' pollen is transferred from bee to bee as they brush against each other in the hive between trips (Free & Williams, 1971a). At least some of this transferred pollen will probably be viable, and such transfers may explain the few fruits that set on trees remote from compatible varieties or where solid blocks of only one self-compatible variety are planted. Transfer of pollen within the hive could also be important when different varieties of a crop are grown for seed in the same locality, and could explain hybridisations over long distances although the bees remain constant to one variety. In fact, the only completely safe way of isolating plants for seed is to grow them in insect-proof glasshouses or cages.

Pollinating efficiency of flower visits

While foraging, nectar-gatherers have a greater proportion of pollen of 'foreign' species on their bodies than pollen-gatherers, but less total pollen (Free, 1966e; Free & Williams, 1971a). Hence, although they may be more important in speciation than pollen-gatherers, they are less likely to deposit pollen on the stigmas of the flowers they visit. The behaviour of many nectar-gatherers also makes them less effective as pollinators. This especially applies to bees visiting extra-floral nectaries, such as on *Helianthus annuus* (Free, 1964c) or *Vicia faba* (Free, 1962b). Visits were most numerous to the extrafloral nectaries of *H. annuus* during the afternoon and of *V. faba* during the forenoon. Few of the bees that visited the extrafloral nectaries of these crops ever made floral visits, although the visits to *H. annuus* extrafloral nectaries became fewer during flowering of the crop. Bees visited the *V. faba* extrafloral nectaries before the flowers opened, were numerous throughout the flowering period of the crop, and increased toward the end of flowering, presumably because the extrafloral nectaries continued to secrete nectar after the floral ones had finished doing so and because there was little pollen left. Therefore, it is especially important that colonies should not be moved to such a crop until the flowers open, otherwise a large proportion of the bees may become conditioned to work the extrafloral nectaries and not pollinate the flowers.

Bumblebees that obtain nectar through holes bitten in the bases of flowers with long corolla tubes do not pollinate the flowers directly, although they may do so by shaking pollen from the anthers onto the stigmas, provided that the flowers are not self-sterile. Although honeybees cannot bite holes, they use the holes bitten by bumblebees, and the numbers of 'robber' honeybees depend on the size of the 'robber' bumblebee population. Most of the honeybees on crops of *Trifolium pratense* (Free, 1958) and *Vicia faba* (Free, 1962b) are often robbing the flowers. Only bees that enter such flowers touch the stamens and stigmas and pollinate them. Often the nectar in the corolla tube is too low for the tongue of a bee to reach it and bees entering the flower collect only pollen. Indeed, they sometimes rob a few flowers of nectar during their foraging trips for pollen.

Individual bees foraging on *T. pratense* or *V. faba* are very constant in behaviour and they either enter flowers to collect pollen only or rob them of nectar. Thus, bees robbing *V. faba* flowers of nectar began working the crop about 4 hours earlier in the day than

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those that only collected pollen. Bees deserted the crop rather than change to a different type of visit, and differences in the relative proportions of the foraging populations on different days, and different times of the day, reflected changes in the bees present and not changes in the behaviour of individuals (Free, 1962b). However, bees foraging on *Phaseolus multiflorus* were more ready to change from robbing the flowers to entering them. Although the increase in honeybee population on the *Phaseolus multiflorus* crop was initiated by the appearance of robber bumblebees, its maintenance was independent of the population of robber bumblebees, and, after the robber bumblebees had disappeared for the season and no more holes were being bitten, many robber honeybees changed to collecting nectar through the mouths of the flowers (Free, 1968c). Presumably honeybees changed their type of behaviour more readily on *P. multiflorus* because they could more easily obtain nectar from the front of flowers than from the other leguminous flowers. Whatever the reason, hole-biting by bumblebees may be advantageous in attracting honeybees to the *P. multiflorus* crop that later enter the flowers and pollinate them. Similarly, the bumblebee's habit of biting holes in *Trifolium pratense* corolla tubes may also be advantageous, because honeybees are often otherwise unable to obtain nectar from the crop and the nectar-gatherers may recruit some pollen-gatherers that pollinate the flowers (Free & Butler, 1959).

Another example of bee and flower being ill adapted to each other is when the corolla tube is too wide and too long. Nearly all honeybees collecting nectar from *Freesia refracta* enter a flower on the side opposite to the stamens and stigma (Free & Racey, 1966), apparently following the prominent nectar-guides (Free, 1970b). Because of the flowers' width such a bee does not touch the stigmas or stamens while approaching the nectaries, though a few touch the stamens as they leave, usually with the ends of their abdomens or the tips of the wings; hence, few if any nectar-gatherers pollinate the flowers.

When visiting other flowers with short corolla tubes, and whose nectar is easily accessible, the behaviour of nectar-gatherers is mostly such as will probably pollinate. For example, nectar-gatherers visiting *Brassica napus* touched the stigmas of a mean of 76% of the 5984 flowers they were watched visiting (Free & Nuttall, 1968a). When visiting a *Ribes nigrum* flower a bee grasps the corolla, or more rarely a nearby leaf, and pushes its tongue and the front of its head between the stigmas and stamens down to the nectaries, so that on each flower visit one side of its head touches the anthers and the other the stigmas. When foraging on *Rubus idaeus*, a bee stands on the petals and stamens and pushes its head and extended tongue between the outer circle of stamens and central stigmas down to the ring of nectary tissue lining the receptacular cup, and, as it follows the ring, one side of its head and body touches the stigmas. Although nectar-gathering bees sometimes land on the petals of a *Fragaria x ananassa* flower and approach the nectary from the side, they nearly always proceed to walk over the stigmas and so may pollinate the flowers (Free, 1968d). However, a nectar-gatherer is not always such an efficient pollinator of tree fruit flowers. It stands either on the anthers or the petals of a flower and pushes its tongue and the front part of its body towards the nectar. When it stands on the anthers, it often touches the stigmas as well as the anthers, and so could pollinate the flower. But when it stands on the petals, it does not touch the stigmas when approaching the nectaries and so could not pollinate the flower; a nectar-gatherer standing on the petals of a flower with spreading stamens (e.g. *Prunus domestica*, *Prunus avium*, *Prunus armeniaca*) has to push past some of the anthers to reach the nectaries, and so may get pollen on its body, but a nectar-gatherer approaching *Pyrus malus* flowers, which have relatively stiff upright stamens, from the side, often does not even touch the anthers and

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so does not get pollen on its body. Nectar-gatherers tend to be constant to one or other type of behaviour (Free & Spencer-Booth, 1964b) and the proportion of nectar-gatherers that approach the nectaries of apple flowers from the top or sides depends on the thickness and length of the filaments. On varieties with relatively short, thin, filaments most nectar-gatherers pushed down to the nectaries from the top of the flower and so could pollinate, but on varieties with thicker and longer filaments the bees apparently had difficulty in reaching the nectaries in this way and approached them from the side and failed to pollinate (Free, 1960).

When visiting many of the species with shallow flowers (e.g. *Prunus* spp. and *Pyrus* spp., *Fragaria x ananassa*, *Rubus idaeus*) some bees deliberately scrabble over the anthers, pulling at them with their legs and biting them with their mandibles, so that their hairy surfaces get covered with pollen which is transferred to their corbiculae. Such bees are valuable pollinators because they always touch the anthers and stigmas.

On many crops, nectar-gatherers also collect some pollen incidentally as they brush against the anthers, although they do not deliberately scrabble for it. Whereas some nectar-gatherers push it into their corbiculae, others scrape it from their bodies and discard it. Some nectar-gatherers foraging on *Helianthus annuus* (Synge, 1947; Free, 1964), *Brassica napus* (Free & Nuttall, 1968a), and *Rubus idaeus* (Free, 1968d) discard pollen. All these crops provide abundant pollen; perhaps this happens with other species but because less pollen is collected incidentally it is less obvious.

The proportions of nectar-gatherers that collect pollen loads differ greatly on different days and different times of the day, and seem to depend on the amount of pollen available (e.g. tree fruits, Free, 1960; Free & Spencer-Booth, 1964b). Although individual nectar-gatherers foraging on shallow flowers such as *Pyrus malus* or *Rubus idaeus* tend to be constant either to discarding or retaining pollen that collects on their bodies, or to scrabbling for pollen (e.g. Free & Spencer-Booth, 1964b; Free, 1968d), the transition between scrabbling and collecting nectar is much easier than on leguminous crops.

The pollinating efficiency of visits by nectar and pollen-gatherers to *Pyrus malus* and *Trifolium pratense* flowers differs. The percentage of flowers of 'James Grieve' and 'Cox's Orange Pippin' that set fruit following a single visit by bees that (a) scrabbled for pollen was 63 and 18 respectively and (b) that did not scrabble for pollen was 45 and 5 respectively (Free, 1966c). The greater success of bee visits to 'James Grieve' than 'Cox's Orange Pippin' can be explained by the ability of 'James Grieve' to set well when self-pollinated. The small set of the 'Cox's Orange Pippin' flowers shows the ineffectiveness of many visits to varieties that need cross-pollination.

The percentage of *Trifolium pratense* florets that set seed after each had received a single frontal visit by bees that collected nectar only, was 20 and by bees that collected pollen, was 46 (Free, 1965a). This large difference was surprising because nectar- and pollen-gatherers enter a flower in the same way and both release the floral mechanism. Perhaps *T. pratense* nectar-gatherers also discard any pollen they collect inadvertently and keep their heads and fossae freer from pollen than pollen-gatherers. This could explain the greater pollinating efficiency of bees with pollen loads.

Although pollen-gatherers are usually more efficient pollinators, they are not invariably so. Honeybees scrabbling for *Helianthus annuus* pollen go to male stage florets and do not pollinate. Honeybees collecting nectar also mostly go to male stage florets, but they stand on the female florets while doing so and so may pollinate (Free, 1964c). In fact, in contrast to most other crops, bees that scrabble for pollen may be disadvantageous because they remove pollen with which nectar-gatherers might become dusted.

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Factors controlling pollen collection and attempts to increase it

Pollen-gatherers are better pollinators than nectar-gatherers of most crops, so increasing the proportion of pollen-gatherers would increase pollination.

One way to do this is to feed colonies sugar syrup. In a series of ten experiments, colonies fed sugar syrup collected two to five times as much pollen as other colonies (Free & Spencer-Booth, 1961; Free, 1964b; Free & Racey, 1966). Further, because pollen-gatherers are more inclined than nectar-gatherers to forage near their colonies, feeding syrup also increased the proportion of pollen-gatherers working the nearby crop. Colonies fed sugar syrup collected more pollen mostly because the behaviour of individual foragers changed, although a greater tendency to collect pollen by bees starting to forage might well contribute to the result (Free, 1965c). When sugar syrup is provided inside the hive, most of the bees that collect it have not foraged previously, and are at the stage of their lives when they would usually receive nectar loads from foragers (Free, 1965d). Therefore, feeding sugar syrup probably creates a shortage of bees ready to receive nectar loads, with the result that nectar-gatherers have difficulty in getting their nectar loads accepted by others; many would, therefore, be discouraged from collecting more nectar and change to collecting pollen. This would explain the rapid change in the behaviour of individual foragers.

Any increased pollination that has resulted from attempts to 'direct' bees to crops by feeding them with sugar syrup containing the scent of the flowers of the target crop, might well come from feeding syrup alone, rather than from the added scent actually 'directing' the bees.

It has been suggested that removing a proportion of the pollen loads of returning foragers by 'pollen traps' at the entrance to hives, might increase the amount of pollen collected. However, the obstruction to foraging the traps create at the hive entrance seems to balance any increase in the proportion of foragers that collect pollen (Free, unpublished).

Adding pollen to colonies decreases pollen collection (Free, 1967a; 1970a), so although feeding a colony supplementary pollen during spring may be valuable in stimulating colony growth, it should not be done when the crop needing pollination is in flower.

Pollen collected by a colony is the source of nitrogen fed to its developing brood (Ribbands, 1953; Simpson, 1955). It is not surprising, therefore, that the presence of brood stimulates foraging in general, but pollen-gathering in particular (Free, 1967a) and that the proportion of foragers of a colony that collect pollen and the amount of pollen collected depends on the amount of brood. Individual bees quickly change from collecting nectar to collecting pollen and *vice versa* in accordance with an increase or decrease in the amount of brood. Hence, colonies to be used for pollination should contain plenty of brood.

Brood of all stages stimulates pollen collection, but sometimes larvae are more effective than pupae. Although access to the brood area is the most important factor stimulating pollen collection, the smell of the brood and contact with bees tending the brood are partly responsible. Perhaps, therefore, adding pheromones produced by brood might increase pollen collection.

As a colony grows the ratio of brood to bees decreases (Free & Racey, 1968b); the relatively larger amount of brood per bee in small than large colonies probably helps to explain why a larger proportion of bees in small colonies usually forage, and why small colonies have less scope than big ones for increasing their foraging when conditions improve (Free & Preece, 1969).

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The presence of a queen stimulates foraging (Free, 1967a), comb production (Free, 1967b) and deposition of nectar and pollen loads (Free & Williams, 1971b), probably because of the pheromones she produces (Butler, 1954, 1967; Butler *et al.*, 1961). Removing the queen decreases the number of loads of pollen collected and many bees collecting pollen subsequently collect nectar only. Because most bees collecting pollen loads also collect nectar, loss of a queen probably diminishes foraging in general. The queen's pheromones are probably less diluted among the bees of small than large colonies, so bees of small colonies receive more stimulus to forage (Free & Preece, 1969) from the relatively greater amount of queen and brood pheromone each receives. Giving additional queen pheromones to colonies might also increase foraging and pollen collection. Queenless packages of bees, in cheap containers, both of which can be destroyed when the pollinating task is complete, could be usefully employed in some circumstances. Synthesised queen pheromones might be used to substitute for a queen in stimulating foraging and comb building in such colonies, but unless a stimulus as powerful as brood is also discovered and used, such colonies are unlikely to forage as efficiently as natural ones (Free, 1967a).

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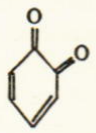
Formation and Behaviour of *o*-Quinones in Some Processes of Agricultural Importance

W. S. PIERPOINT

This review is concerned with a group of reactions that occur in living and decaying organisms and are thought to involve *o*-quinones. The reactions affect some agricultural and food-producing processes, and are relevant to problems studied in several departments at Rothamsted.

Quinones, so called because they derive from quinic acid a component of cinchona bark, are cyclic α-β unsaturated diketones. The two ketone groups are, usually, part of a six-membered ring of carbon atoms, and can occupy two positions relative to each other. These are the ortho- and para- positions and are exemplified in *o*-benzoquinone (I) and *p*-benzoquinone (II)



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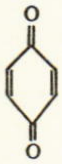
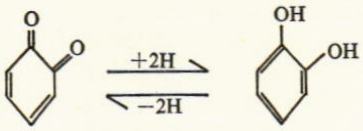


II

The nomenclature emphasises the aromatic compounds to which the quinones can be converted either by reduction or as a result of substitution into the six-carbon ring



The ease with which this conversion occurs differs from one quinone to another. It depends on attached groups that may stabilise either the quinone or the aromatic form, but usually goes more easily with *o*-quinones. Thus these compounds are the more reactive and the more powerful oxidising agents. *o*-Benzoquinone, for example, polymerises rapidly in water; it was not prepared till 1904, 66 years after *p*-benzoquinone was isolated, when Willstater devised a completely anhydrous method of oxidising catechol. This difference in stability between *o*- and *p*-quinones is reflected in the mode of occurrence and metabolic functions of the two types of quinones.

p-Quinones have been isolated from many living organisms. Some are widespread and, because of their reversible reducibility, may be essential cellular components. A family of isoprenoid substituted *p*-benzoquinones, aptly called ubiquinones, function as hydrogen carriers in the respiratory cytochrome systems of many, if not all, aerobic cells. Similarly the related plastoquinones are hydrogen carriers in photosynthesis, and phylloquinone, a derivative of *p*-naphthoquinone is a vitamin, K_1, in higher animals. Also, more than 200 *p*-quinones of more restricted distribution have been isolated from flowering plants, fungi, lichens and insects. They include derivatives of *p*-benzo, naphtho-,

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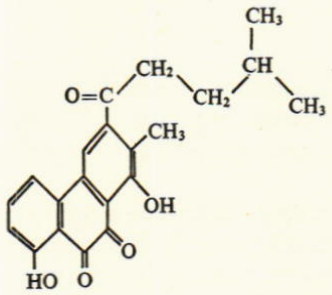
and anthroquinone, and some are peculiar to a given species. They are regarded as secondary metabolic products and, except for those with antibiotic properties, their metabolic significance is uncertain.

In contrast, only about half a dozen *o*-quinones have been isolated from organisms. They are, typically, red fungal pigments of limited interest in which the *o*-quinone structure is stabilised by fused benzene rings, as in piloquinone from *Streptomyces pilosus*.



The reactivity of *o*-quinones seems not only to make them less likely than *p*-quinones to occur as metabolic end products, but also less likely to be stable extractable components of metabolic pathways. In the reactions, metabolic or post-mortem, that concern us, they occur only as transient intermediates, whose formation has been demonstrated by trapping them with suitable reagents. In many reactions they have not been trapped; their formation is inferred from the known mechanisms of similar reactions.

Enzymic formation of *o*-quinones and their subsequent reactions

The reactions that produce *o*-quinones are the oxidation of phenols, generally *o*-dihydroxyphenols, by polyphenoloxidases. Suitable phenols are widespread in biological tissue, and plants characteristically contain derivatives of cinnamic acid, such as chlorogenic acid (Fig. 1), or flavanols such as epicatechin (Fig. 4). The polyphenoloxidases, copper-containing proteins, are also widespread if not strictly ubiquitous. Some of them oxidize only selected *o*-dihydroxyphenols, although the *o*-quinones produced may oxidize other compounds and, in the process, be reduced to the original phenol. Others, usually the tyrosinases, not only oxidize dihydroxyphenols, but convert monohydroxyphenols, such as tyrosine, to oxidizable dihydroxyphenols. Other systems, enzymic and non-enzymic, oxidize dihydroxyphenols but do not produce *o*-quinones. Reactions catalysed by the laccases, for example, proceed by single electron-removing steps and produce semi-quinones, whose subsequent behaviour differs from that of *o*-quinones.

Once formed, *o*-quinones react non-enzymically with many compounds. They may polymerize, be reduced, or suffer nucleophilic attack by substances possessing amino, thiol and 'activated' methylene groups. In all but the simplest or controlled systems therefore, they are liable to undergo a mixture of initial reactions. Even in simplified systems there are secondary reactions, often involving more quinone, whose course may critically depend on the concentration of quinone, relative amounts of other reactants and acidity. It is difficult therefore to summarise these reactions briefly, especially in a way applicable to more than one or two quinones. Reaction schemes in Fig. 1 and 2 can be regarded only as simplified summaries of the initial reactions that quinones undergo. They are based on reactions suggested for chlorogenoquinone, the *o*-quinone derived from the oxidation of chlorogenic acid by tobacco-leaf polyphenoloxidase. Their formulation

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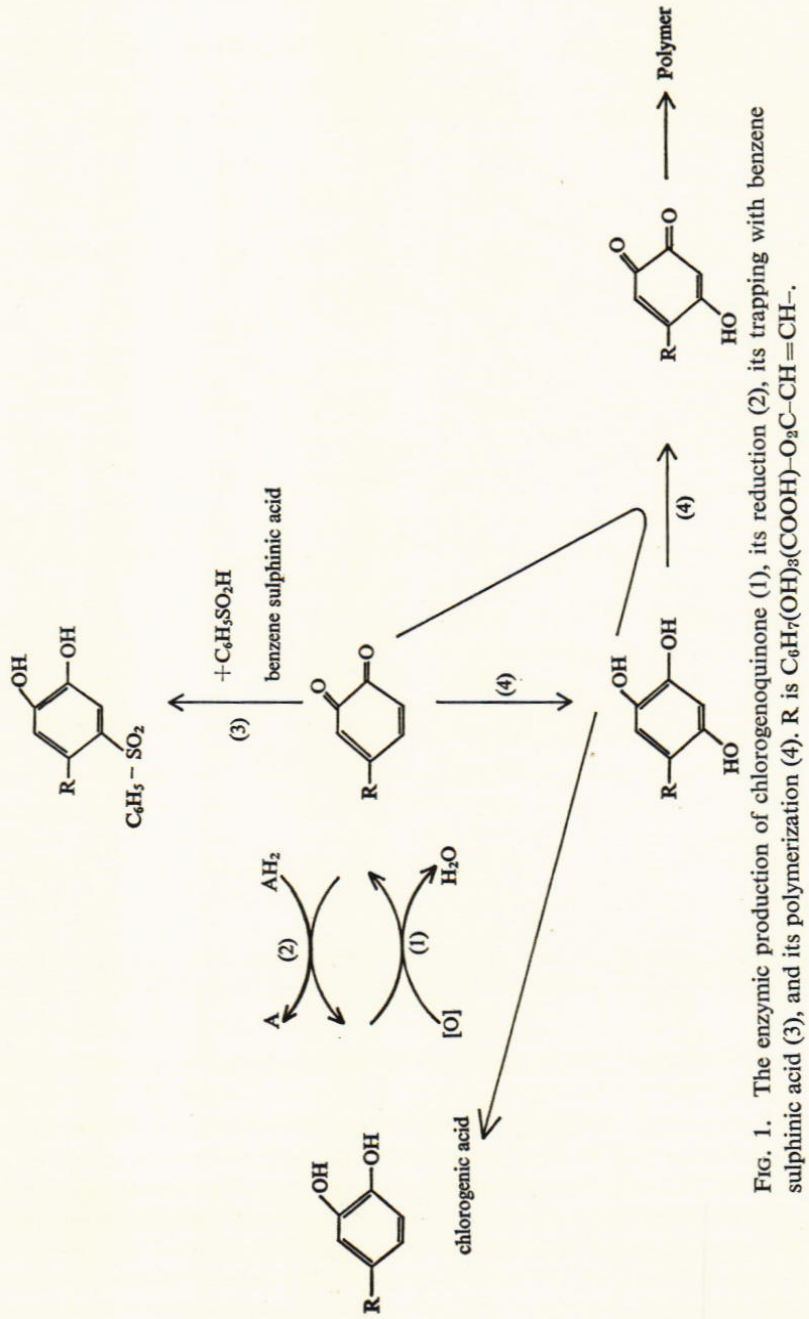

FIG. 1. The enzymic production of chlorogenoquinone (1), its reduction (2), its trapping with benzene sulphinic acid (3), and its polymerization (4). R is $C_6H_7(OH)_3(COOH)–O_2C–CH=CH–$.

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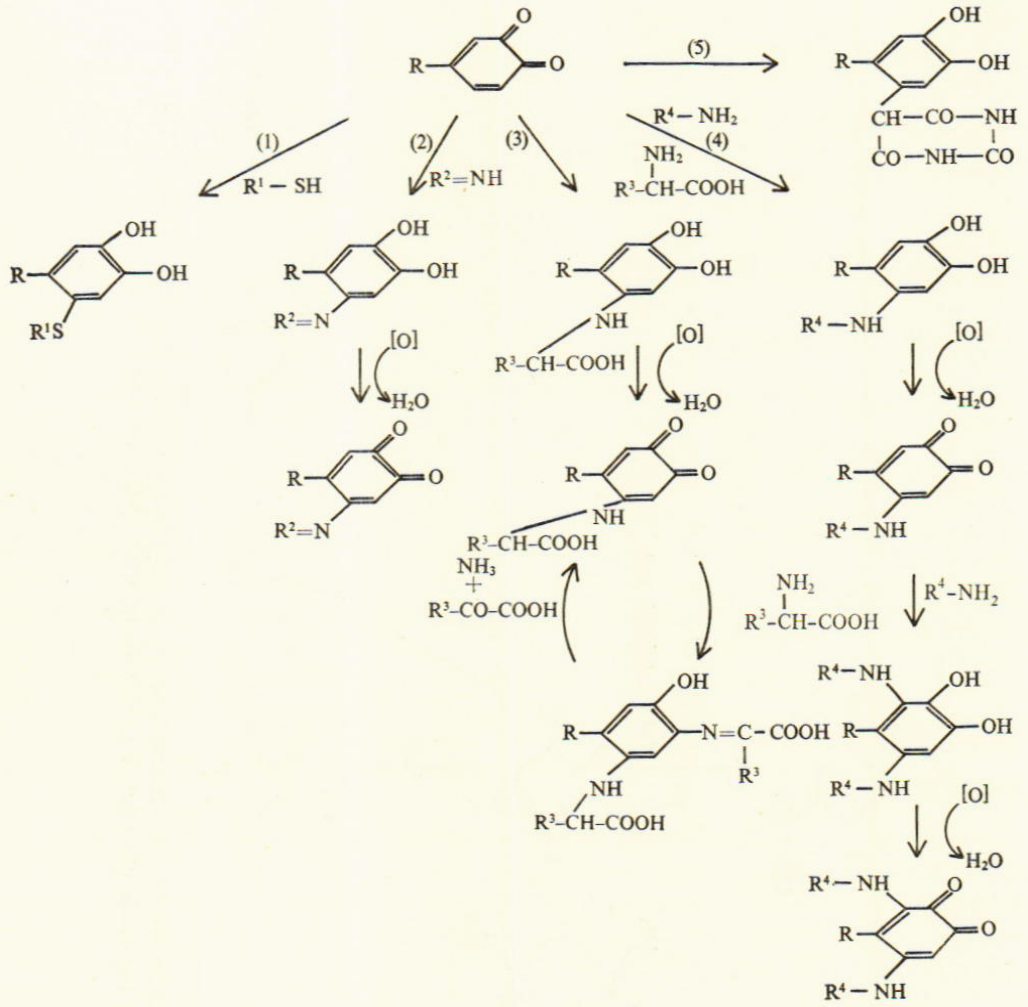

FIG. 2. Probable course of reactions of chlorogenoquinone with thiol compounds (1), amino acids with secondary amine groups (2), amino acids (3), amines (4), and the active methylene group of barbituric acid (5).

(Pierpoint, 1966; 1969a; 1969b) relies heavily on analogies with reactions of simpler quinones (Mason, 1955).

Enzymically-generated chlorogenoquinone is reconverted to chlorogenic acid by reducing agents (AH_2; Fig. 1) such as ascorbic acid, reduced coenzymes, and in part by —SH compounds. The reaction goes readily enough, but, for some quinones, is accelerated by an enzyme from peas. As the chlorogenic acid can be reoxidised, this provides a system for the continuous oxidation of AH_2 and for delaying the accumulation of quinone; the rates of both reactions follow a complex course because reducing agents partially inhibit polyphenoloxidases. The reaction of the quinone with benzene sulphinic acid has no biological significance, but it is included in Fig. 1 as an example of the trapping reactions used to demonstrate the formation of *o*-quinones *in vitro*. When the sulphinic acid is in excess, the oxygen absorbed is restricted to that involved in the formation of the quinone. The sulphones formed are stable enough to be isolated and identified. In

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the absence of reducing and trapping reagents, chlorogenoquinone polymerises to brown, poorly defined pigments. The reactions may (Fig. 1), by analogy with those suggested for *o*-benzoquinone (Wagreich & Nelson, 1938), involve water and an oxidation by more quinone. Similarly by analogy, the polymers may contain aromatic rings directly linked or joined to alkyl groups through ether bonds.

The reactions between chlorogenoquinone and amines, amino acids, thiol compounds and compounds with reactive methylene groups are formulated (Fig. 2) as if the primary point of attack was the 6′ position; this, *a priori*, seems probable, and in the reaction with benzene sulphinic acid almost certain. The mono-substituted products are aromatic and probably colourless: that derived from barbituric acid is stable, as are those from some thiol compounds unless there is a large excess of quinone. Other primary products, such as the aminohydroquinones, are further oxidized, probably by more chlorogeno-quinone, to coloured quinoid forms. The reaction stops here with secondary amines such as proline, and the products are stable enough to be identified spectrophotometrically, even though not to be isolated. The quinone substituted with primary amines, e.g. aniline, however, is further substituted and oxidized to give a disubstituted quinone, and this may be repeated until all the available positions on the chlorogenoquinone are occupied. Disubstitution may occur with amino acids also (Fig. 2), but the course of this reaction is obscured by secondary reactions in which the monosubstituted quinone oxidatively deaminates excess amino acid. Trautner and Roberts (1950) describe an imaginative and feasible way in which this might occur.

Proteins have a range of chemical groups, amine, α-amino and thiol, potentially able to react with *o*-quinones. Although some of these will be 'buried' in the interior of the protein and consequently unreactive, exposed groups will probably be reactive because of their peptide bonding. Cross links may be formed between different parts of the protein, as reactive groups from different parts of the peptide chain attack either the same quinone molecule (e.g. –NH–Q–NH–) or different ends of a group of polymerizing quinone molecules (–NH–Q–$(Q)_n$–Q–NH–). Not only would this alter the biological properties of the protein but it may alter its gross physical properties. This, of course, is what happens when collagen and proteins of hides are converted to leather by treating them under denaturating conditions with chemical tanning-agents such as *p*-benzo-quinone.

There is another possible course for the reaction between quinones and proteins. The polymers formed from some phenols, especially the flavanols, might have 'tannin-like' properties, and, as do the classical vegetable tannins, complex with and possibly precipi-tate proteins. These reactions would depend initially on hydrogen-bonding between phenolic groups and peptide bonds, and be reversed by detergents or alkali. However, they would become less reversible with time as *o*-quinone groups form in the phenol and react covalently with suitable groups on the proteins. The end products therefore may well be difficult to distinguish from those formed directly from proteins and polymerizing *o*-quinones.

Because of the reactivity of *o*-quinones, the coexistence of polyphenoloxidase and oxi-dizable *o*-dihydroxyphenols in a single cell is potentially suicidal. Clearly mechanisms are required to control the oxidations or prevent them. Necessary contact between these enzymes and their substrates, as for example when polyphenoloxidases hydroxylate monophenols, is probably controlled by the redox balance of the cell: an enzyme has been described that reduces *o*-quinones at the expense of reduced coenzymes. There are other ways of controlling these reactions or of preventing them occurring prematurely. Thus the oxidation of phenols to melanins in mammalian pigment cells is restricted to

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membrane-bound organelles, and the polyphenoloxidase of some insect tissues occurs as inactive pro-enzyme. Similarly the polyphenoloxidase of phenol-rich *Vicia faba* leaves exists in a masked condition (Kenten, 1957), and many plant phenols are converted to more stable esters and glycosides. Enzymes and substrates may also be separated in plant cells, although the evidence for this is not conclusive. Many of the claims that plant polyphenoloxidases are contained in specific cell components are open to doubt (Sanderson, 1964), and little is known of the intracellular location of polyphenols.

Whatever control mechanisms may operate in a plant cell, they are removed when the cell is injured. Phenolic compounds are then oxidized and *o*-quinones produced. These may react with cell constituents increasing the injury, or polymerize to brown or other dark coloured products. This accidental production of *o*-quinones is as relevant to our subject as their controlled metabolic production. When it occurs in part of a tissue as a result of a local injury we will call it adventitious, and when as a general reaction of a dying organism, post-mortem. These three types of reactions, metabolic, adventitious and post-mortem, somewhat arbitrarily separated, will serve as three convenient classes in which to consider some of the reactions involving *o*-quinones.

Metabolic processes involving *o*-quinones

Of the metabolic roles that have been suggested for *o*-quinones, some, such as a respiratory function, are doubtful, and others, including tropolone synthesis, are of limited interest. The most relevant of the remainder is their role in reinforcing wall structures. They seem not to be involved in the synthesis of lignin; although this synthesis involves the oxidative coupling of phenols, it requires peroxidases or laccases and the intermediates are semi-quinones. *o*-Quinones, however, are almost certainly involved in the sclerotinization of exoskeletons and egg cases of arthropods, and in the melanization of seedcoats, spore walls and pigment cells of many other organisms.

Fresh cuticles of many arthropods, especially insects, as well as the walls of egg capsules, are pale soft structures. They are mainly proteinaceous, although the exoskeletons contain also the polysaccharide chitin. Over a period of hours, they harden and darken into leathery, rubbery or horny membranes of great mechanical strength and chemical resistance. Pryor (1940) emphasised that, during this process, for which he coined the term sclerotinization, they accumulated much (20–40% dry weight) phenolic material, including *o*-dihydroxyphenols. He argued that the process was, in fact, a quinone-tanning; that *o*-quinones produced by the oxidation of the phenols cross-linked the protein chains into rigid lattice structures.

There is evidence from several insects to support this idea, and to indicate how the process is controlled. For instance, immediately before they pupate, the larvae of the blowfly (*Calliphora erythrocephala*) accumulate much *N*-acetyl dopamine (*N*-acetyl-3,4-dihydroxy-phenyl-β-ethylamine) in the blood. This is produced from tyrosine under the influence of the hormone ecdysone. Ecdysone also seems to activate a latent polyphenoloxidase located in or near the cuticle. Conditions are thus established for an *o*-quinone to form where it can diffuse into and sclerotinize the cuticle. The tanning of the egg capsule of the cockroach (*Blatta orientalis*) is similarly brought about by the quinone derived from 3,4-dihydroxybenzoic acid. This phenol is secreted as a 4-*O*-β-glucoside, along with polyphenoloxidase and the protein that forms the egg wall, by one of a pair of glands that discharge into the egg pouch. However, tanning starts only when a glucosidase is secreted by the other gland and hydrolyses the glucoside into an oxidizable dihydroxyphenol.

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The reactions between the quinones and the cuticular proteins are poorly understood because little is known of the untanned proteins themselves, many reactions are possible, and the products are difficult to analyse. The picture of the process is necessarily vague and based largely on inference from simpler systems. Usually, but not always, the proteins involved contain little S, and free amino groups become fewer during the reaction. The primary reactions probably involve terminal amino groups, and then lysine ϵ-amino groups, to give amino hydroquinones which are converted to coloured amino quinones. Quinone bridges linking protein amino groups, such as –NH–Q–NH– and –NH–Q–Q–Q–NH–, are then possible depending on the availability of substitutable positions in each quinone molecule. These bridges may also link protein to any unacetylated amino groups in chitin. How many such bridges exist, and which groups they predominantly connect, is unknown, but tanned cuticle is so rich in phenol that, if much of it exists as polymer, penetrating the interstices of the proteins, not many bridges would be needed to confer rigidity on both the protein and the chitin.

Another type of bridge has been suggested that may cross-link peptide chains in tanned insect cuticles. It is based on tyrosine residues in the proteins, which, if accessible, may be hydroxylated by insect polyphenoloxidases to *o*-diphenols and further oxidized to *o*-quinones. These may condense with each other, with nearby amino groups or with tanning quinone. This possibility has received little attention. But cuticle protein is rich in tyrosine, and much of it seems to be altered chemically during sclerotinization. More germane perhaps, biphenyl linkages, such as would be produced by the condensation of adjacent oxidized tyrosine residues, have been identified in resilin, a remarkably rubber-like protein that forms wing-hinges of some insects (Andersen, 1966).

Fragmentary evidence suggests that some cuticles and outer membranes of nematodes are also tanned by *o*-quinones. Phenols have been detected, chemically and histochemically, in the outer cuticular layers of both adults and larvae in several species (e.g. *Ascaris*). However, the pale colour of these cuticles, and their digestion by the proteolytic enzyme papain, argue against much tanning. There is more tanning in the egg-coat and cyst-wall of the potato cyst eelworm (*Heterodera rostochiensis*). Both contain 2–3% of phenols that are liberated on hydrolysis (Clarke, Cox & Shepherd, 1967; Clarke, 1968). Moreover the cyst-wall, in its formation from the body wall of the female, shows the colour and textural changes associated with sclerotinization, and possesses a polyphenoloxidase.

Sclerotinisation alters the properties of the cyst-wall, including its permeability to water, and undoubtedly contributes to the remarkable longevity (up to eight years) of these cysts in soil (A celebrated Shakesperean clown also attributed the preservation of tanned bodies in soil to their impermeability to water (*Hamlet*, Act V, Scene 1).) Besides this structural role, the phenols and quinones of the wall may well aid in hatching of the eggs; wall fragments double the hatchability of *H. rostochiensis* eggs (Shepherd & Cox, 1967), and synthetic quinones, including *o*-naphthoquinone, stimulate the hatching of *H. schachtii* eggs (Clarke & Shepherd, 1964).

A special case of cell wall reinforcement is when the phenolic component is a derivative of dihydroxyphenylalanine (dopa). The protein complex is then a dark pigment containing polymerized indole structures and known classically as melanin. Plant melanins occur typically in seed coats and the walls of fungal spores. They undoubtedly contribute to the durability of these bodies: the resistance of wall preparations from *Aspergillus*, *Rhizoctonia* and *Sclerotium* spp. to lysis by added enzymes or by soil bacteria is related to their melanin content (Kuo & Alexander, 1967). However, the melanins of plant tissues are less well characterized than those of animals. These, as the main pigments of

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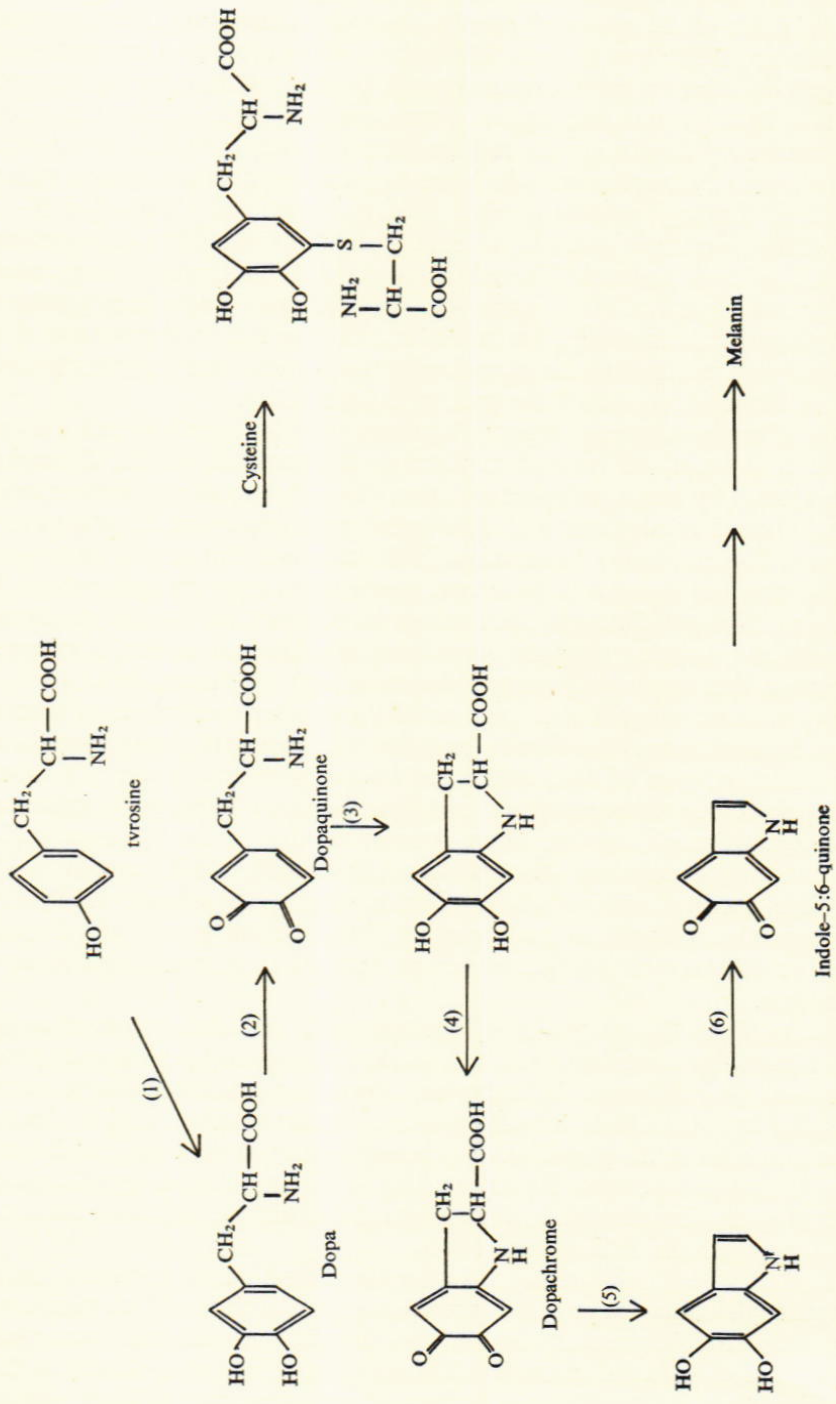

FIG. 3. The formation of melanin by the oxidation of tyrosine. Reactions (1) and (2), and possibly (4) and (6) require polyphenoloxidase. Also shown is the reaction of dopaquinone with cysteine which is believed (Nicolaus *et al.*, 1969) to give rise to a family of pigments which decorate red human hair and the feathers of New Hampshire chickens.

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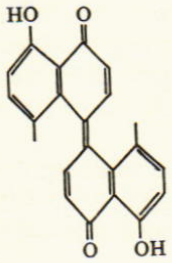
vertebrate hair and skin, have attracted much attention; they pose both intricate chemical problems and urgent social ones.

The first stages in melanin formation probably involve three oxidations of dihydroxyphenylalanine by polyphenoloxidase, and three distinct *o*-quinones (Raper, 1938). The first, dopaquinone, reacts intramolecularly (Fig. 3), the amino group of the side chain substituting into the quinone nucleus to produce a bi-cyclic compound. This is oxidized to the second quinone, dopachrome, which in turn, after decarboxylation, is oxidized to indole-5,6-quinone. There is little certainty about subsequent stages; indole-5,6-quinone alone polymerizes to black insoluble substances, but in natural melanins these are linked both to protein and to metals. The quinones probably form an irregular three-dimensional lattice in which each quinone unit has multiple links, and which is attached to proteins predominantly through –S– atoms. Some of the quinone units may be derived from dopaquinone or dopachrome; some of them may, as electron spin resonance studies suggest, be free-radical semi-quinones.

Wall strengthening polymers based on phenols and quinones other than dopa and dopachrome have been recognised in plant walls, especially those of fungi. The dark pigments of sunflower and melon seeds are, for example, probably derived from catechol (Nicolaus *et al.*, 1964): the black 'melanochitin' that is partly responsible for the nickname (King Alfred's Cakes) of the fungus *Daldinia*, is an extended *p*-naphthoquinone polymer:



It is probably cross-linked to unacetylated amino groups of chitin, and polyphenoloxidase is probably involved in its formation (Allport & Bu'Lock, 1958). Probably many other pigments, loosely called melanins because of their appearance and reaction in hi to-chemical tests, will prove also to be derived from phenols other than dopa, and not, strictly speaking, melanins at all. There seems a need for a new general term, analogous to sclerotins, to describe all such materials derived from plant cell walls by the interpolation of polymerizing phenols. The term melanin, as lignin, could then be restricted to polymers derived from one phenol.

Adventitious production of *o*-quinones

The antimicrobial properties of phenols and quinones have long been known and made use of, so it is not surprising that the phenols and *o*-quinones of plants should have been considered as part of the plant's defences against infecting organisms. This idea receives support from the increased phenol and polyphenoloxidase of diseased plants; it has the added attraction that differences between the phenols of different species and varieties of plants may partially account for one of the salient facts of plant pathology—the host specificity of many parasites. These ideas, and the comparative ease with which phenols having antimicrobial activity can be extracted from many plants, have led to an immense literature. However, there are as yet very few examples in which phenols or quinones are clearly and unequivocally responsible for resistance to disease.

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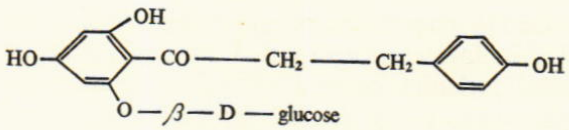
One such example is the resistance of onions to the smudge disease fungus *Colletotrichum circinans*. Spores of this fungus germinate on the skin of the onion, penetrate the dead outer scale leaves, and then grow into and parasitize the fleshy leaves of the bulb. Many resistant varieties of onion have red or yellow outer scale leaves, but their resistance depends on the *o*-dihydroxyphenols, catechol and protocatechuic acid, in the cells of the dead outer scales and not on the anthocyanin pigments. These phenols prevent infection by inhibiting the germination of spores. How they do this, and whether they need to be oxidized to quinones, is not known.

Other host-parasite interactions show no such simple relation between resistance and the presence or absence of a particular phenol. Resistance may be conferred by a larger concentration of a substance that occurs in all varieties, or the presence of a mechanism that must be triggered to expose the parasite to this substance. The first explanation has been invoked for the resistance of potatoes to the scab fungus (*Streptomyces scabies*) and to *Verticillium* wilt. Scab-resistant varieties grown in U.S.A. contain more chlorogenic acid than do susceptible ones, and it is mainly concentrated in the periderm of young, rapidly growing tubers, especially round the lenticels through which the fungus invades. Similarly, wilt-resistant varieties have more chlorogenic acid in the vascular tissue of underground stems and only lose their resistance as it disappears. Chlorogenic acid, in amounts less than those estimated to occur in potato sap, stops the *in vitro* growth of both *S. scabies* and *V. albo-atrum*, and the germination of spores of *V. albo-atrum*. Moreover, it does so more in conditions in which it is slowly oxidized. However, there are many difficulties in the way of accepting the idea that chlorogenic acid, or oxidizing chlorogenic acid released from damaged cells, controls the fungal invasion; surveys of European potatoes (e.g. McKee, 1958) show no relation between scab-resistance and phenol content.

Careful studies suggest that the phenol and polyphenoloxidase of young apple leaves confer some resistance against the apple-scab fungus, *Venturia inaequalis*. The main phenol in these leaves, which may account for 4–8 % of their fresh weight, is phloridzin:



It is hydrolysed to the aglycone phloretin by a leaf glucosidase, and both these phenols are hydroxylated to *o*-diphenols and oxidized to *o*-quinones by polyphenoloxidase. The balance between these reactions is complex and depends on the pH of the leaf sap (Raa, 1968), but there is no appreciable difference between those occurring in the sap of scab-resistant and susceptible leaves. However, some intermediates of the oxidation, most probably *o*-quinones, are fungicidal; and there are reasons for thinking that they are formed and affect the growth of *V. inaequalis* only in resistant leaves.

The hyphae of scab fungus proliferate between the epidermis and cuticle of susceptible leaves without penetrating the host cells or, in the first stages, causing their collapse. By contrast, cells of resistant hosts rapidly collapse and die around the primary invading hyphae. This 'hypersensitive' reaction stops the growth of the fungi, possibly because it allows the production of *o*-quinones. This quinone-producing mechanism is thus an anti-infection device common to both susceptible and resistant leaves, but which is triggered off only in resistant ones. Proteins have been isolated from culture filtrates of *V. inaequalis* that do cause necrosis in resistant leaves. Curiously enough they seem to be melanoproteins.

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'Hypersensitive' reactions are important resistance mechanisms in many plants. Rapid collapse of cells is enough to prevent the growth of many parasites, but the concomitant oxidation of phenols to *o*-quinones and polymers may also discourage saprophytic organisms that would otherwise grow on dead tissue. Even when these compounds do not affect the pathogen directly, they may inhibit the 'tissue-macerating' enzymes it secretes to facilitate its spread.

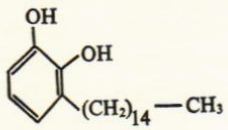
Although some macerating enzymes, especially polygalacturonases and others that depolymerise pectin are only slightly affected by simple polyphenols, they are strongly inhibited by oxidized chlorogenic acid and catechins, the substances that accumulate in browning tissue. This inhibition probably occurs naturally, and the resistance of apple varieties to the spread of the brown-rot fungus (*Sclerotinia fructigena*) from wounds, is proportional to the rate at which they discolour. Moreover resistance is decreased by painting the wounds with substances, such as glutathione, that prevent browning. Very little of the active polygalacturonase secreted by fungi can be recovered from the fungus-rotted tissue.

The fungi that produce the soft white rots of apples, in particular *Penicillium expansum*, seem to have a mechanism that prevents these inhibitory polymers from forming. They are thought to produce substances, some possibly derived from the phenols of the apple tissue, which inhibit polyphenoloxidase (Walker, 1969). Much pectin is broken down in these infections, and polygalacturonase can be isolated from the rotted tissue. In spite of this, *P. expansum* lesions spread slower than those of brown rots, which suggests that if *S. fructigena* develops an anti-browning mechanism it might be even more aggressive.

Infection by viruses can also affect the metabolism of phenolic compounds by plants. Indeed, chemical tests for phenols have often been suggested as methods of diagnosing some infections, although these have not proved satisfactory (e.g. Holden, 1957). It has also been suggested that the oxidation of phenols restricts the intercellular movement of viruses, much as it is thought to do for *V. inaequalis*.

Necrotic lesions are often associated with the localisation of virus in a leaf. They have been regarded as hypersensitive responses in which a metabolic upset has allowed the oxidation of phenols, and this has killed the cells and stopped virus movement. Farkas, Kiraly & Solymosy (1960) showed that infections producing local necrotic rather than systemic symptoms, greatly increase the polyphenoloxidase of leaves, and that infiltrating leaves of *Nicotiana glutinosa* with the reducing agent ascorbic acid decreased the number of lesions produced by tobacco mosaic virus, without appreciably affecting the multiplication of the virus. But, however good the evidence that phenols are involved in lesion formation, it is unlikely that the necrosis prevents the movement of virus: Bawden (1964) describes many instances where it does not, and also some where virus is localised without necrosis.

A different type of defence mechanism, the chemical warfare waged against animals by poison ivy and poison oak, probably involves *o*-quinones. The active substances produced by poison ivy (*Rhus toxicodendron radicans*) are 3-pentadecyl catechol and related compounds with ethylenic links in the side chain:



These are primary skin irritants, but more important they act as haptens, and produce allergic responses. The most likely mechanism for their conversion into antigens is that

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once inside the animal, they are oxidized to *o*-quinones which react with serum proteins: such quinone–protein complexes have been made *in vitro* and their antigenicity demonstrated. *Rhus vernicifera*, the Japanese lac tree, produces the same or similar phenols, but uses them less aggressively; they are in the latex, and when exposed to air are oxidized by a latex enzyme to hard insoluble polymers. These probably protect the wounds of damaged trees: in manufactured lacquers they both protect and decorate furniture.

Post-mortem production of *o*-quinones

I. Possible role in the formation of humus. As vegetable matter decays in the field, and its cellular structure disintegrates, most of its *o*-dihydroxyphenols will be oxidized. The resulting quinones will polymerize and, in doing so, combine with other cell constituents, especially proteins and amino acids. The products are likely to be heterogenous and to include some of the partial structures already indicated. As they are added to the top layers of the soil, their structure will be modified by oxidative and hydrolytic activities of microorganisms. There are, however, some reasons for thinking that quinone-protein polymers are not quickly degraded as are proteins (Bremner & Shaw, 1957); they are more resistant than proteins to many hydrolytic enzymes. This has encouraged the idea that polymerized quinones, combined with proteins and amino acids, survive in the soil and contribute to its relatively stable humus component.

Opinion on the chemical structure of these humic materials is not unanimous. The highest common factor of many opinions is that they are a mixture of amorphous three-dimensional polymeric acids of high molecular weights, with aromatic, partly quinoid structures, and with a range of molecular sizes. They are unexpectedly rich in amino acids, which account for as much as a third to a half of soil nitrogen (Bremner, 1955) and which *in situ* are probably linked by peptide bonds. These amino acids, in addition to other compounds that can be removed by hydrolysis in 6N HCl, 'turn over' in soil much faster than does the non-hydrolysable aromatic nucleus; the average age of the hydrolysable components of Broadbalk top soil, sampled from the unmanured plot in 1881, is 510 years compared to 2560 for the non-hydrolysable fraction (Dr. D. S. Jenkinson, personal communication). Some of these properties are, at least, consistent with the idea that humic materials are derived from heteropolymers of proteins and quinones. Model compounds prepared by polymerizing *o*- and *p*-quinones in the presence of proteins such as casein (Ladd & Butler, 1966) show an encouraging resemblance to humic acids. They behave similarly during chromatography on columns of Sephadex, and, on acid hydrolysis, produce amino acids, ammonia and unreleased N. Moreover, their amino acids, as those of humic acid, are slowly released by some fungal proteases: it would be interesting to know whether the polymers remaining after losing their amino acids can combine with, or otherwise 'pick up', fresh protein or quinone-proteins, as soil humus seems to do.

If quinones are involved in the genesis of humic materials, they need not only be those derived from plant *o*-dihydroxyphenols; soil microorganisms may produce and oxidize their own phenols. Swaby and Ladd (1963) and Flaig (1960) outlined two distinct ways in which this could occur. The phenols may be synthesised intracellularly from carbohydrate substrates, polymerize with proteins as the cells decay, and be released into the soil only as the cell walls are lysed. Alternatively, the reactions may be extracellular, at least in part, as when the microorganisms hydrolyse and oxidize plant lignins. Lignins are themselves polymerized phenols derived from coniferyl alcohol and related compounds, but most of their hydroxyl groups are methylated. However, as they decompose

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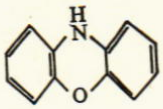
in soil they lose their methoxy groups and concomitantly bind N. Flaig argued that the demethylation is hydrolysis by fungal enzymes, and that N is bound when *o*-dihydroxyphenols are produced from the polymer and oxidized to quinones that react with ammonia, amino acids or proteins. Some of these reactions have been reconstructed *in vitro*, and suggest that the products include, in addition to structures already mentioned, amino phenols or amino quinones that may polymerize to heterocyclic aromatic structures such as phenoxazines:



But how far such structures contribute to soil organic matter is unknown.

About a tenth to a sixth of the organic sulphur of soil is present as α-amino acids, which, on acid hydrolysis, yield methionine, methionine sulphoxide, cystine and cysteic acid. They probably occur in peptide form, and possibly in quinone-protein heteropolymers. If this is so, there is the additional possibility that some soil sulphur exists as cysteine linked to a quinone nucleus through its S (Fig. 2), in addition to, or instead of, its N. Little is known of the stability of these S–C bonds, although some of those in melanin resist acid hydrolysis (Nicolaus *et al.*, 1964). This possibility is worth consideration therefore, even if very little of the S in a plant is present as –SH able to combine with quinones: some protein –SH groups have great affinity for quinones, and stable compounds accumulate in soil even though added in small amounts.

2. Formation of *o*-quinones during the preparation and storing of food materials. Cellular injuries inflicted during the harvesting, processing and storage of plant materials cause oxidation of any phenols present and the polymerization of *o*-quinones. These 'enzymic' browning reactions (so called to distinguish them from non-enzymic ones, such as those that occur on heating proteins and sugars) adversely affect the value of most fruits and vegetables, spoil their colour and flavour and, by the reaction in Fig. 1, decrease their vitamin C content. The phenols most usually implicated are caffeic and chlorogenic acids as these are most readily oxidized, although oxidized flavanols are reported to produce most of the brown discoloration in apples and pears. Browning may occur in canned, frozen and even dehydrated materials, and much effort has gone into devising methods of preventing it. These include quick heating or blanching, which is designed to inactivate enzymes, excluding air, and adding substances such as sulphite or ascorbate that inhibit polyphenoloxidases or combine with quinones.

Reactions of *o*-quinones with proteins in plant protein concentrates may decrease their nutritional value. The biologically-measured nutritional value of many such feeding stuffs is less than that predicted from their known amino acid contents; some amino acids seem unavailable to animals although they are liberated by the hydrolysis in 6N HCl that precedes amino acid estimations. Lysine is often biologically unavailable in this manner, which is important because it is one of the amino acids deficient in many diets. Probably its ε-NH_2 is involved in linkages stable to enzymic digestion but broken by acid hydrolysis, and some of these linkages may involve *o*-quinones. The biological value and *in vivo* digestibility of casein are decreased by reaction with caffeoquinone and chlorogenoquinone (Horigome & Kandatsu, 1968): and lysine–quinone bonds, as those between other amino acids and quinones (Ladd & Butler, 1966), are probably partially hydrolysed by acid.

The nutritional value of plant protein concentrates is often also limited by methionine,

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which is both scarce and 'unavailable'. However, it is less probable than with lysine that this is because it reacts with *o*-quinones. *o*-Quinones may oxidize it to methionine sulphoxide but this would not necessarily decrease its biological usefulness. Reactions that might do so by oxidizing it to a sulphone or forming S^+–quinone bonds have been postulated, but preliminary efforts to demonstrate them with chlorogenoquinone and methionine have failed.

Bound quinones are most likely to occur in proteins extracted from tissues rich in phenols. They may well affect the quality of leaf-protein concentrates that have been advocated (Pirie, 1969) as dietary supplements. Feeding tests show that the nutritive value of these preparations is usually good but varies with the species and age of the leaves that have been extracted. Poorer samples tend to have more of their lysine ϵ-NH_2 unreactive towards nitrous acid (Dr. R. L. M. Synge, personal communication), suggesting that part of the loss in nutritive value may reflect reactions with quinones: there is ample opportunity for these reactions during the large scale extraction. The *in vitro* digestion of these leaf protein preparations with proteolytic enzymes has been used (e.g. Byers, 1967) to judge their biological value. These tests also are likely to be affected by protein-bound quinones: the susceptibility of dried pasture plants to pepsin depends on the *o*-dihydroxyphenol and polyphenoloxidase content of fresh leaves (Horigome & Kandatsu, 1968). However, these tests, especially those that use plant proteolytic enzymes, are not necessarily affected by bound quinones in the same way as is biological digestibility. Thus papain and ficin, in contrast to carboxypeptidase and trypsin, are not inhibited by polymerized quinones, but in some conditions stimulated (Ladd & Butler, 1969).

Not all the phenolic oxidations and *o*-quinone reactions in agricultural products are deleterious: the processing and desired characteristics of beverages and stimulants such as tea, cocoa, cider and tobacco depend on them. This is most evident with black tea. Although the main reason for drinking tea is ostensibly the stimulation derived from its caffeine, most of the expertise that goes into producing acceptable tea is concerned with its phenolic content. Agricultural aspects are designed to produce leaves rich in both phenols and polyphenoloxidase: the critical conditions of fermentation are designed to allow the enzyme to oxidize the phenols, allow the *o*-quinones produced to condense to coloured polymers and to stop the process at that point. These polymers confer on brewed tea its colour, most of its palate, and some of its odour. When their formation is prevented, as in green teas, the brew is, by comparison, pale and insipid.

Because of the many types of phenols in the leaves of the tea plant, and the many possible interactions of the corresponding *o*-quinones, it could reasonably have been expected that the chemical reactions are enormously complex. However, E. A. H. Roberts pointed out: (1) that the main difference between fermented and unfermented leaf lay in the disappearance of epigallocatechin (Fig. 4) and its gallate ester; (2) that compounds resembling the main soluble condensed phenols in brewed tea can be produced *in vitro* by oxidizing these two substances; (3) that the condensed phenols are probably dimers of these catechins uncombined with amino acids.

Fig. 4 shows a scheme by which one of the main groups of tea pigments, the theaflavins, is probably formed. It differs a little from the scheme of Roberts, and it envisages the oxidation of both epigallocatechin and catechin (Takino *et al.*, 1964). The theaflavin formed by the condensation of the catechin *o*-quinones has a seven-membered tropolone ring. Either one or both of the hydroxyl groups on the O-containing rings may be esterified with gallic acid, and these esters probably form a larger proportion of tea theaflavins than does the unesterified compound. The other main group of tea pigments, the redder,

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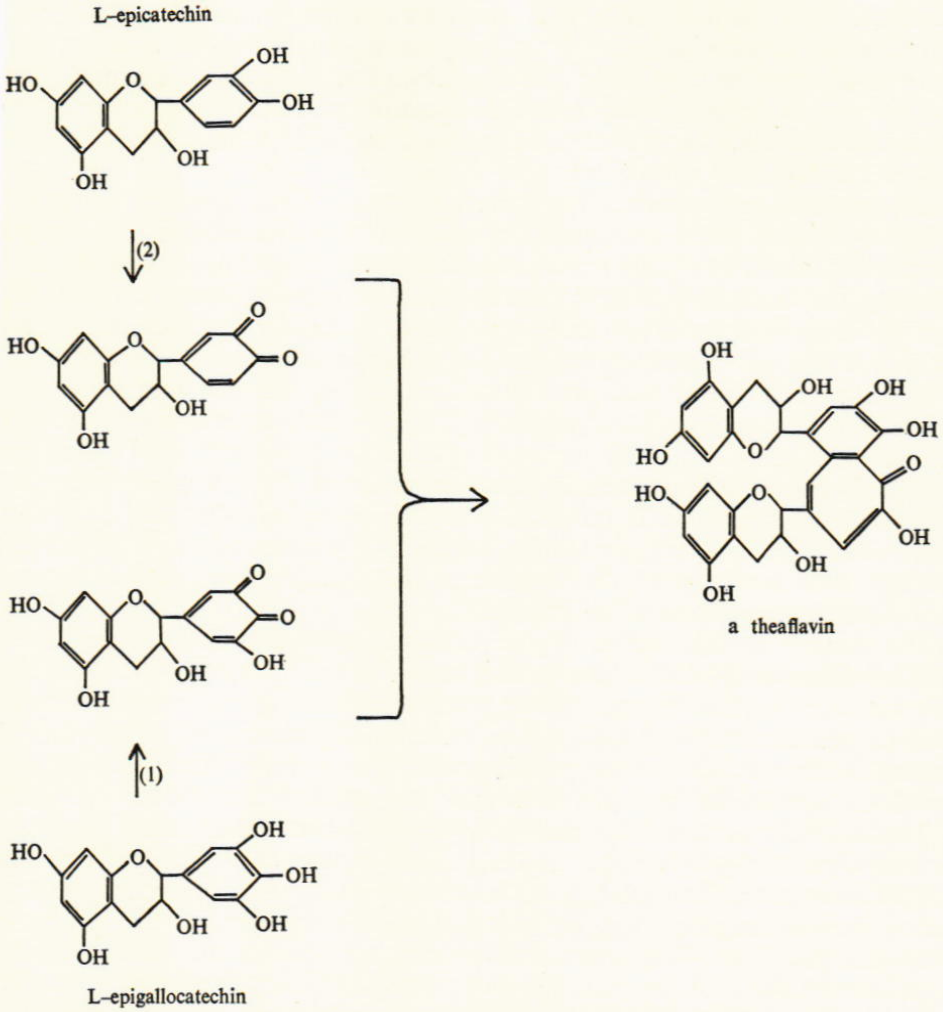

FIG. 4. Reaction scheme for the formation of theaflavins, orange coloured astringent pigments, during the fermentation of tea (after Takino *et al.*, 1964). Reactions (1) and (2) are catalysed by polyphenoloxidase.

less astringent thearubigins, are less well characterised, but they probably contain polymerized catechin groups, some in the oxidized *o*-quinone form.

Although the main pigments of brewed tea seem not to contain N, reactions between *o*-quinones and nitrogenous compounds occur during fermentation and may contribute to the quality of the manufactured product. Thus, the aldehydes, especially phenylacetaldehyde, which are partly responsible for the aroma of tea are probably produced by the quinone-catalysed oxidative deamination of amino acids.

3. Formation of *o*-quinones in the laboratory. A third, rather more specialised, environment in which plants may die, and where the *post mortem* formation of *o*-quinones occur, is the laboratory. Whether the vegetable matter is ground, homogenised, disintegrated or macerated, provided it contains polyphenoloxidase and oxidizable phenols, and conditions do not completely and immediately inactivate the enzyme, some *o*-quinone will

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be formed. Even when the enzyme is inactivated, some *o*-quinone may be produced in extracts alkaline enough (pH $>$ 8) for the phenols to auto-oxidize. When enough has been formed to remove most of the reducing substances, the extract will probably brown. The brown materials often complicate the estimation and isolation of other substances in these extracts: when the substances in question react with *o*-quinones there is an extra hazard not always fully appreciated.

These reactions may produce new species of comparatively small compounds, such as quinone-peptides, which complicate the difficult task of characterising the non-protein N fraction of leaves. They may remove substances that are being searched for, and, less expectedly, they may artificially produce them. Both these last effects are possible with the growth substance indol-3-yl acetic acid (IAA). In slightly acid solution, *o*-quinones react with IAA to give inactive compounds of unknown constitution: those from chlorogenoquinone are intensely red. By contrast, in slightly alkaline solution *o*-quinones produce IAA by reaction with tryptophan. The reaction is an example of the catalytic deamination of amino acids by *o*-quinones (Trautner & Roberts, 1950) already mentioned, followed by the spontaneous decarboxylation of the keto acid produced. It is questionable whether IAA is produced this way physiologically, but its production complicated efforts to detect a protein-bound and slowly released form of IAA in extracts of French Bean leaves, where the *o*-quinones that catalyse it are derived from novel esters of caffeic acid (Wheeler & King, 1968).

Many enzymes are more active in plant extracts prepared by methods minimising the oxidation of phenols, probably because they react with and are inactivated by *o*-quinones. A few such enzymes, for example sucrose synthetase from sugar cane and phosphorylase from potatoes, are sensitive to synthetic quinones and are inactivated *in vitro* when added polyphenols are oxidized by polyphenoloxidase. This type of inactivation is, initially at least, distinguishable from that caused by preformed tannins or quinone polymers with tannin-like properties. It has been variously attributed to the reaction of *o*-quinones with amino or sulphydryl groups of the protein or with a prosthetic group such as pyridoxal phosphate. Sometimes, as with sucrose synthetase, the reaction seems partly reversed by –SH reagents, implying that the quinone oxidizes protein –SH to –S–S– instead of forming an –S–hydroquinone adduct, but none of the inhibiting reactions has yet been studied with the precision that protein chemistry currently allows. Perhaps this is why this type of inactivation is often overlooked, or when recognised causes surprise. Some enzyme studies demand that it is not overlooked; if it is, attempts to measure enzymes in different physiological states of a tissue may simply measure differences in the amounts of inhibitory *o*-quinones different extracts produce.

By a rare piece of biochemical justice, polyphenoloxidases themselves react with and are affected by the *o*-quinones they produce. Purified preparations from various sources contain fractions whose colour suggests that they contain some bound quinone material, which increases as they are allowed to oxidize an appropriate substrate. Reaction with quinones probably explains the progressive inactivation of polyphenoloxidases during an oxidation: 'reaction inactivation' is decreased when the oxidation produces a substituted *o*-quinone less likely to react with proteins.

The extraction of cell organelles from plant tissues is also complicated by enzymically produced *o*-quinones, and requires conditions that avoid phenol oxidation. This is so for extracting the mitochondria of sweet potato tubers (*Ipomoea batatas*), the chloroplasts of sugar cane leaves (*Saccharum officinale*), and various plant viruses. All, once extracted, are sensitive to added phenols plus polyphenoloxidase, and most of them to synthetic *o*-quinones. Rather surprisingly more is known about the inactivation of the viruses.

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Thus the inactivation of cucumber mosaic virus, by oxidizing chlorogenic acid, is not caused by the oxidation of phenolic residues in the virus or by the polymerized products of the oxidation, but involves an intermediate of the oxidation that probably reacts with the protein rather than the nucleic acid of the virus (Harrison & Pierpoint, 1963; Pierpoint & Harrison, 1963). Prune dwarf virus reacts with synthetic *o*-benzoquinone, and the uninfected particles retain the morphological and serological properties of the virus (Hampton & Fulton, 1961). Tulare apple mosaic virus reacts not only with *o*-benzoquinone but also with such fully substituted derivatives as tetrachlorobenzoquinone. Mink (1965) argued that the inactivation is therefore caused by the oxidation of a viral group rather than by adduct formation. However, he also showed that the tetra substituted derivatives form adducts with the virus, and not only inactivate it but progressively modify its sedimentation, spectral and serological properties. Possibly the amino and thiol groups of the protein displace the halogen atoms from the substituted quinones.

Only a minority of known plant viruses seem to be inactivated by the *o*-quinones formed in leaf extracts. This may mean that it is advantageous for a virus to be insensitive to these compounds, or that the sensitive ones have been overlooked. However, the fact that viruses are not inactivated does not necessarily mean that they do not react with *o*-quinones, and there is evidence that southern bean mosaic virus reacts with *o*-quinones without losing its infectivity. This apparent *tolerance* to *o*-quinones contrasts with the *resistance* of some strains of tobacco mosaic virus. Neither intact TMV, nor its depolymerized protein, can be induced to react with chlorogenoquinone, although each protein subunit contains one thiol and two amino groups. This emphasises that, because of the differences in molecular architecture, the amino and sulphydryl groups of different proteins differ in accessibility to, and affinity for, *o*-quinones, as they do for other reagents.

Table 1 lists five principle ways of preventing *o*-quinones forming in plant extracts, although it is not always easy to judge why a technique is effective. Polyvinylpyrrolidone, for example, was initially used in enzymic extraction because it absorbs tannins strongly, but it absorbs simple *o*-dihydroxyphenols much less strongly and owes some of its efficacy to inhibiting polyphenoloxidase. Similarly DIECA, a powerful oxidase inhibitor, also combines with *o*-quinones, and conversely, the reducing agent ascorbate also inhibits polyphenoloxidase. Cysteine, depending on the conditions, combines with quinones, reduces them to phenols and inhibits the oxidase.

All the procedures listed have been effective in protecting some particular plant component from *o*-quinones. None is generally useful. The reducing agents, for example, are rapidly oxidized by some tissue extracts and DIECA and potassium ethyl xanthate break down in acid extracts. None of the enzyme inhibitors is specific for polyphenoloxidase; those that chelate metals affect other metal-dependent enzymes, and metabisulphite, although very effective for some purposes, affects pyridoxal phosphate and probably enzymes containing this cofactor. Disrupting tissues in an N_2 atmosphere is cumbersome; although it can be done much more conveniently in a specially designed press (e.g. Pirie, 1961) than in a glove box, it may still involve the difficulty of working up the resulting extract anaerobically. The choice of the most appropriate method, or combination of methods, for preventing *o*-quinones being produced, depends very much on the tissue used, the phenolic systems it contains, and the component that is to be recovered. It is very much a matter for trial and error.

There is a final caution: the phenol content of frozen leaves stored between 0 and −15°C slowly decreases, and the possibility exists that *o*-quinones are formed, and react with some leaf components even in these conditions. This is probably also true for unfrozen

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TABLE 1

Methods of preventing o-quinones forming in plant extracts

Principle	Technique	Example
Exclude oxygen	Disrupt tissue in N_2 atmosphere	Extraction of bulk leaf protein
Remove polyphenols	Extract tissue with solvents	Washing acetone powders of leaves
	Absorb phenols onto polymers: polyvinylpyrrolidone (PVP) insoluble PVP (polyclar AT) polyethylene glycol albumin	Extraction of enzymes from apple fruit and leaves of peppermint (*Mentha piperita*, L.)
Inhibit polyphenoloxidase	Extract tissue in: trichloroacetic acid sodium diethyldithiocarbamate (DIECA) potassium ethylxanthate thioglycollate metabisulphite	Extraction of amino acids from leaves Extraction of viruses from leaves of tobacco (*Nicotiana tabaccum*) and enzymes from tubers of potatoes (*Solanum tuberosum*)
Reduce quinones	Extract tissue in ascorbate	" " " " "
Trap quinones	Extract tissue in: cysteine benzene sulphinic acid	Extraction of enzymes, including polyphenoloxidase, from acetone powders

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but senescing tissue. Even though such tissue is then extracted so as to prevent further *o*-quinone formation, these components will have been modified. Some plant enzymes that can be resolved electrophoretically into several active components may owe some of their multiplicity to this reaction: it is important to distinguish such artifacts, if they occur, from physiologically separate isozymes.

Summary

o-Quinones are often produced as transient intermediates when *o*-dihydroxyphenols are enzymically oxidized. They polymerize rapidly to compounds whose complexity depends on the *o*-quinone involved and the presence of substances containing amino or sulphydryl groups with which they react. Some of the heteropolymers they form, insect cuticles, melanins and possibly humus, are very complex: because of the range of repeating units and different linkages they contain, it is not certain whether they have a regular recognisable molecular structure or resemble, in Freundenberg's phrase, 'chemical compost heaps'.

o-Quinones are formed and polymerize *in vivo* during the hardening of arthropod cuticles (sclerotinisation) and the hardening of plant seed and spore walls (melanisation). They are also formed adventiously, as when plants are invaded by microorganisms, and either mechanically or chemically may help restrict the multiplication or spread of the pathogen. Their formation during the harvesting, storing or processing of plant materials affects, for good or ill, the quality of the product, and the polymers they produce during the decay of vegetable matter may be the parent substances of soil humic matter.

Unless precautions are taken, *o*-quinones can form in plant extracts made in the laboratory. Their subsequent reactions may complicate or even prevent the extraction and estimation of organelles, enzymes, viruses and metabolites.

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Docking Disorder and Root Ectoparasitic Nematodes of Sugar Beet

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Docking disorder takes its name from the parish in N.W. Norfolk where patches of stunted sugar beet were first reported in 1948 (Hull, 1949), although it almost certainly occurred earlier there and elsewhere on light sandy soils. Typically, affected seedlings grow slowly, soon show signs of nutritional deficiencies, especially of magnesium and nitrogen, and the rootlets are discoloured and misshapen. The condition recurs in the same fields and the same areas in fields, but its severity differs greatly from year to year. Other crops, such as barley, often grow poorly where sugar beet was previously affected.

Anything that damages the roots can, of course, slow the growth of plants and lead to nutritional deficiencies. Hence, it is not surprising that the early work on Docking disorder, done in different places, led to seemingly contradictory conclusions or that the role of ectoparasitic nematodes as a prime cause took long to establish, even though the beneficial effects of treating soils with 'D-D' fumigant were early shown (Shotton, 1958).

The name 'Docking disease' (Gates, 1954) was changed to 'Docking disorder' when Gates (1955) concluded that fungi (*Pythium*, *Fusarium* and *Rhizoctonia*), which were prevalent in the damaged roots of affected sugar beet plants, were not the cause, and suspected a toxin, but Skinner (1956) found no evidence for this. *Fusarium oxysporum* and *Pythium* sp. damaged roots of sugar beet growing in pots, but not enough to account for the effects in the field (Buxton, 1957). Drenching the rows with fungicide at the time of sowing sugar beet improved root shape (Gates, 1955) but possibly not by killing fungi. The organic manure 'shoddy' (wool waste) greatly increased the vigour and yield of sugar beet where Docking disorder occurred, but farmyard manure and inorganic nitrogen gave less consistent improvement (Shotton, 1958; Hull, 1960).

Christie and Perry (1951) described stubby root nematode (*Trichodorus* sp.) damage in the U.S.A. Gough and Welford (1954) suspected these nematodes might be involved but failed to correlate their abundance with Docking disorder, probably because methods of extracting ectoparasitic nematodes from the soil were less good then than now. Gibbs (1959) isolated fungi and nematodes from affected roots but these did not differ in type or number from those isolated from unaffected roots. Also, affected beet taken from the field recovered when replanted in compost whereas beet grew poorly in pots containing the field soil even after it was autoclaved. He suggested the poor growth depended on an unusual chemical or physical condition in the soil; this may have been so, as the soil he used came from the edges of marl pits or from slopes, contained very little clay or organic matter, and slaked completely when moistened.

The soil-borne viruses tobacco rattle (TRV) and the Scottish form of tomato black ring (TBRV-S) were first isolated from sugar beet growing in eastern Scotland (Harrison, 1957; Cadman & Harrison, 1959), but seemed not responsible for the poor growth. TRV is transmitted by stubby root nematodes—*Trichodorus pachydermus* Seinhorst in the Netherlands (Sol & Seinhorst, 1961) and *T. primitivus* Seinhorst in Britain (Harrison, 1961; Mowat & Taylor, 1962). TBRV is transmitted by needle nematodes—*Longidorus elongatus* (de Man) in Scotland (Harrison, Mowat & Taylor, 1961) and *L. attenuatus* Hooper in England (Harrison, 1964). The knowledge that these viruses occur in some

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plants in areas where sugar beet grows poorly in East Anglia, but that most of the stunted plants are not infected (Gibbs & Harrison, 1964; Heathcote, 1965), and the report that *Trichodorus* damaged sugar beet in the Netherlands (Kuiper & Loof, 1962), led to a reassessment of the relationship between nematodes and Docking disorder.

Types and symptoms of Docking disorder

Gibbs and Harrison (1963) separated Docking disorder into three 'types': (i) diffuse patches of poorly growing plants with needle nematodes (*Longidorus*) present; (ii) 'kite'-shaped patches; (iii) edges of disused marl pits. Whitehead (1965) added two 'types': (iv) areas of excessive drainage; (v) cultivation effects and Whitehead, Greet and Fraser (1966) added another: (vi) diffuse patches of poor growth with *Trichodorus* present. We now restrict the name to one condition, patches of stunted plants caused primarily by *Longidorus* and/or *Trichodorus* feeding on the seedling roots (i.e. (i) and (vi) above). Stunting of beet for other reasons, such as when growing at 'edges of disused marl pits', in 'areas of excessive drainage' or when suffering from 'cultivation effects' should be so described. The reason for stunted plants in the 'kite'-shaped patches recognised by Gibbs and Harrison (1963), Gibbs (1966) and Macfarlane (1966, 1967) is unknown, and the condition was renamed 'Barney patch' from its first recognition at Barney, Norfolk (Dunning & Cooke, 1967).

The plant and field symptoms of Docking disorder are fairly characteristic (Dunning & Cooke, 1967; Jones & Dunning, 1969). Patches of affected plants are ill-defined but coincide roughly with the areas of lightest soil; within the patches most sugar beet plants are very small ('chicks') but some are larger and a few ('hens') may be as large as healthy plants outside the patches. The large and small plants are usually randomly intermingled except where cultivation effects, especially tractor 'wheelings', produce lines of large plants. The leaves of small plants often show signs of magnesium and, especially, nitrogen deficiency.

Where *Trichodorus* spp. predominate, the seedling tap root is often badly injured and may be killed; the laterals then take over its function, leading to a fangy (furcated) storage root. Where *L. attenuatus* predominates, only the laterals are injured, leaving the storage root of normal shape, though small. Hence a fangy root is not characteristic of Docking disorder; conversely anything that kills the tap root (e.g. *Rhizoctonia solani* infection, mechanical damage (Daniels, 1965), acidity, damage by chemicals (Hull, 1960) excessive compaction or waterlogging of the soil) can produce fangy roots. Considerable numbers of *Longidorus* or *Trichodorus* need to be found in the root zone of stunted plants to confirm the poor growth as Docking disorder.

The amount to which a given population of nematodes damages roots depends on their activity, which is much influenced by soil moisture. Damage that could be compensated for when roots are growing vigorously cannot be in soils of poor structure or lacking nutrients, or when plants are harmed by herbicides.

Incidence of Docking disorder

Before 1958 Docking disorder was rarely reported outside West Norfolk and was sometimes confused with toxicity from γ BHC seed dressing; the N.A.A.S. and British Sugar Corporation recorded that it was most prevalent in 1948, 1949, 1954 and, especially, 1953, but was not reported in 1950, 1956 and 1957. In 1958 it occurred more extensively (Gibbs, 1959) but in the early 1960s damage by herbicides sometimes made identification

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difficult. Since 1963, fieldmen of the British Sugar Corporation have estimated with increasing accuracy the acreage affected (Table 1).

TABLE 1

Docking disorder in England, 1963–70

Year	Acreage estimated affected (acres)[1]	Estimated loss of root yield (tons)[2]
1963	400	—
1964	1200	—
1965	900	—
1966	1300	—
1967	6000	21600
1968	2300	2300
1969	19250	50000
1970	520	600

[1] Based on monthly pest damage reports from each fieldman of the British Sugar Corporation: 1963–66, acreages severely to moderately affected; 1967–70, total acreages of severely, moderately and slightly affected at the end of June.

[2] Assuming losses of 6 tons roots/acre (severely affected), 3 tons/acre (moderately affected) and 1 ton/acre (slightly affected).

Badly affected crops are occasionally ploughed in and the land sown with another crop, but root ectoparasitic nematodes alone rarely kill the seedlings. Since records became more accurate the acreages reported affected have varied greatly in different factory areas and different years (Table 2).

TABLE 2

Acreage estimated affected by Docking disorder in six sugar factory areas

	1964	1965	1966	1967	1968	1969	1970
East Anglia							
King's Lynn	255	111	40	1600	200	4240	0
Wissington	153	62	10	188	50	1015	5
Bury St. Edmunds	515	592	2	789	194	1832	20
Cantley	45	5	15	96	0	710	15
Yorkshire							
York*	8	6	1201	1451	170	2280	0
Selby*	9	28	16	1200	321	1750	470
	985	804	1284	5324	935	11827	510

* Much stunting not recognised as Docking disorder before 1966

Although only recently recognised in Yorkshire, we think Docking disorder caused by *Trichodorus* spp. was prevalent there earlier, because in 1965 we found several infested fields, two of which had more than 8000 *T. anemones*/litre of soil in the root zone of stunted plants during autumn. Docking disorder has now been reported from most areas where beet is grown on sandy soil, and it seems more prevalent than formerly. Partly, this reflects increasing recognition, but in 1967 and 1969 symptoms were severe. In 1969 it was reported from 14 of the 18 sugar factory areas and eight had more than 1000 acres affected (Bury St. Edmunds, Ipswich, King's Lynn, Newark, Nottingham, Selby, Wissington and York). It can occur after almost any field crop, including grass or after a year's fallow; it is rare after lucerne (Hull, 1960), and is commonest after barley because barley usually precedes beet in the rotation.

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Methods of growing sugar beet have changed greatly since Docking disorder was first noted and these changes may have contributed to its apparent increase. Sugar beet seedlings are now exposed longer to the attacks of nematodes because of early sowing, and to more nematodes per seedling, because of wider spacing and the use of rubbed and graded or monogerm seed, instead of natural (multigerm) seed. Pre-emergence herbicides not only kill weeds on which the nematodes might otherwise feed but can also slow the growth of beet seedlings (Hull, 1966) and may make them suffer more from nematode damage. Damage may be enhanced by the depletion of organic matter, resulting from the replacement of livestock and leys by cereals, and from straw burning and deep ploughing (Hull, 1960).

The nematodes

Species and damage. Kuiper and Loof (1962) associated *T. teres* Hooper (syn. *T. flevensis* Kuiper and Loof) with stunting, fangy roots and yield loss in sugar beet on new polder soil in the Netherlands. Evidence that *L. attenuatus*, *L. elongatus*, and *Trichodorus* spp. damage sugar beet and other field crops in England was obtained: (i) by showing that these nematodes caused specific types of root damage on sugar beet seedlings growing in pots containing steamed soil inoculated with the nematodes; (ii) by observing the nematodes feeding on the roots of seedlings in glass-sided boxes; (iii) by relating the abundance of nematodes around the roots during spring and early summer with root symptoms and stunting of field plants (Table 3) (Whitehead, 1965, 1966, 1969; Whitehead & Cooke, 1965; Whitehead & Hooper, 1970).

TABLE 3

Average numbers of Longidorus *or* Trichodorus *in the soil close to sugar beet plants of different sizes growing in parts of fields affected by Docking disorder*

Number of fields examined	Close to stunted plants	Close to larger plants
	L. attenuatus/litre of soil	
25*	143	70
	L. elongatus/litre of soil	
3	335	104
	Trichodorus spp./litre of soil	
24	2200	800

* In ten of these fields there were on average only 31 *L. attenuatus*/litre in the soil close to large plants in parts of fields *unaffected* by Docking disorder.

Longidorus spp. (needle nematodes) are among the largest plant-parasitic nematodes; many adults exceed 5 mm long and to the naked eye are visible adhering to plant roots. *Trichodorus* spp. (stubby root nematodes) are smaller, the adults usually shorter than 1 mm and invisible to the naked eye. Both *Longidorus* and *Trichodorus* feed on root tips.

Longidorus spp. have long feeding stylets that are probably inserted deeply into roots; presumably in response to saliva injected, the root tip swells and later may show a necrotic spot, probably where the stylet was inserted. Sections of root tips galled by *L. attenuatus* show a row of necrotic cortical cells, extending deep into the root tip, marking the probable region of stylet penetration. *L. elongatus* can stop the tap roots of beet seedlings growing, whereas *L. attenuatus* usually harms only the lateral roots. Both cause galls on sugar-beet roots. *L. elongatus* also damages strawberries (Sharma, 1965; Seinhorst, 1966),

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grass, carrots, kale and probably many other crop plants (Whitehead, 1969; Whitehead & Hooper, 1970).

Trichodorus spp. have shorter stylets that penetrate less deeply than those of *Longidorus* spp. Their feeding often stops tap roots growing. The terminal and lateral root tips become stubby (i.e. stunted and slightly swollen), turn brown or black and laterals may be zig-zagged. When the tap root stops growing or is killed, lateral roots near the soil surface thicken and replace it. When *Trichodorus* are abundant, the downward-growing laterals also are injured and laterals grow only near the soil surface, where conditions are less favourable for the nematodes. Although a shallow root system is a common result of *Trichodorus* injury, effects differ because of the influence of secondary pathogens or soil conditions. Saliva injected by feeding nematodes seems to cause only local damage, and the leaves show symptoms because the damaged roots do not supply them with enough nutrients.

When sugar beet seedlings injured by *Longidorus* or *Trichodorus* are washed free from soil containing the nematodes many injured roots resume growth and new rootlets form close to those which were killed. Hence, in the field, plants may recover when the nematodes stop feeding on the roots, as during a dry spell (Whitehead & Hooper, 1970).

Other plant-parasitic nematodes are common in fields where Docking disorder occurs and may add to the damage caused by *Trichodorus* and *Longidorus*. *Pratylenchus* spp. and *Tylenchorhynchus* spp. multiply greatly on barley, which usually precedes sugar beet on light, sandy soils. *P. minyus* Sher and Allen occurs sporadically in the roots of stunted sugar beet and may feed ectoparasitically on the roots. *Tylenchorhynchus dubius* Bütschlii does not cause obvious lesions on sugar beet roots and seems to feed mostly on root hairs (Whitehead & Hooper, 1970). *Hemicycliophora similis* Thorne were found attached by their stylets to swollen root tips of sugar beet seedlings in the Docking area of Norfolk (Whitehead, 1967).

Soil sampling and extraction. To relate the abundance of ectoparasitic nematodes to injury, crops must be sampled at the correct time, because fewer occur in soil taken near the roots of small seedlings as the season advances and more near the roots of larger plants, which provide more feeding sites. The abundance of ectoparasitic nematodes was related to injury by taking soil samples from mid-May onwards in the rows close to large and small seedlings, and at 2-inch (5 cm) intervals away from the plants at right angles to the crop rows. The numbers on the roots are related to the damage and some estimate of these was obtained by lifting seedlings carefully, washing their roots in water and counting the nematodes in the water and still attached to the roots. The seedlings, their roots and the adhering soil, were weighed and the number of nematodes per gram calculated. Some species, e.g. *H. similis* and *L. elongatus*, remain firmly attached to sugar beet roots when taken from soil, and *L. attenuatus* sometimes remain close to the roots on which they have been feeding, by coiling or by getting entangled in root hairs or fungal hyphae. *Trichodorus* is easily dislodged because it is short, does not coil and its stylet does not penetrate deeply. Later in the season, when the root systems are larger and the soil usually drier, many roots are broken and so many nematodes are dislodged when plants are lifted that the method cannot estimate the number feeding on the roots.

It is almost impossible to estimate total populations of ectoparasitic nematodes in soil. Eggs are laid singly, must be extracted by centrifugal flotation (Flegg & McNamara, 1968) and can be identified only when they have a characteristic shape, as those of *Longidorus* spp., and only when one species of each genus is present, which is rare.

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Identifying the larvae, either within eggs or soon after hatching, is difficult. Also, even the best methods rarely extract more than three-quarters of all stages. Nevertheless, suitable methods extract larvae and adults consistently and are adequate to compare numbers around healthy and diseased plants, to follow changes with time or depth, and to assess the effects of such control measures as the use of nematicides.

Small ectoparasites, such as *Tylenchorhynchus* spp., *Tylenchus* spp. and *Paratylenchus* spp., were best extracted by a Baermann method (Whitehead & Hemming, 1965) but this was unsuitable for *Trichodorus* and *Longidorus*. *L. attenuatus* and *L. elongatus* from sandy soils and *L. elongatus* from peat soil were extracted satisfactorily by decanting a suspension of soil in water onto a sieve with 100 μ apertures submerged under a constant head of water. The two-flask method (Seinhorst, 1955) extracted *Trichodorus* spp. satisfactorily from sandy soils (Whitehead & Hooper, 1970).

Geographical and depth distribution. Seven species of stubby root nematodes (*Trichodorus anemones* Loof, *T. cylindricus* Hooper, *T. pachydermus* Seinhorst, *T. primitivus* Seinhorst, *T. similis* Seinhorst, *T. teres* Hooper and *T. viruliferus* Hooper) and four species of needle nematodes (*Longidorus attenuatus*, *L. elongatus* and occasionally *L. caespiticola* Hooper and *L. leptocephalus* Hooper) occur in fields where beet suffer from Docking disorder. Two or more of these species often occur together in the same field. Five species of *Trichodorus* have been found in one field.

The commonest species of *Trichodorus* in sandy soils prone to produce Docking disorder are *T. pachydermus* and *T. primitivus*, but *T. cylindricus* and *T. teres* are abundant in some places. *L. attenuatus*, the commonest needle nematode in such soils in eastern England, also occurs in the Midlands in sandy soils but is uncommon in the low-lying sandy soils of the Vale of York, where *Trichodorus* is abundant. *L. elongatus* is abundant in some Fen peat soils and in sandy soils in the West Midlands, but is rare in the drier sandy soils of eastern England (Whitehead & Hooper, 1970).

The girth of *Trichodorus* spp. and *Longidorus* spp. restricts them to major soil passages. The surface 2 inches (5 cm) of light, sandy soils where *L. attenuatus* and *Trichodorus* spp. stunt sugar beet may contain few nematodes during late spring or early summer, when the soil is drying, but there may be many 2–8 inches (5–20 cm) deep (Cooke & Draycott, 1970). *T. teres* was most abundant 5–10 cm deep in polder soil (Kuiper & Loof, 1962) and *T. cylindricus* more abundant above plough depth than below it; by contrast *L. attenuatus* was often more abundant below plough depth (Whitehead & Hooper, 1970). Drying of the top soil early during the growing season can prevent the nematodes from moving and feeding, whereas deeper down they can still be active.

Bionomics. Species of *Trichodorus* and *Longidorus* can feed on the roots of many plants but seem to multiply to different extents under the same crops in different seasons and in different places (Taylor, 1967; Whitehead, 1967; Cooke & Hull, 1967; Whitehead & Hooper, 1970; Whitehead, Fraser & Greet, 1970). They can survive a long time without food so they are not greatly affected by bare fallowing (Harrison & Hooper, 1963; Whitehead & Hooper, 1970).

L. elongatus, *L. attenuatus* and *T. teres* are parthenogenetic, but other *Trichodorus* spp. have functional males. There are four larval stages and development from egg to adult ranges from a few months to a year or more. They also multiply slowly, so the populations are diminished for a long time after the soil is fumigated (Whitehead & Tite, 1968; Cooke, Draycott & Hull, 1969; Whitehead, Fraser & Greet, 1970).

The use of herbicides and 'drilling to-a-stand' means there are fewer roots than

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previously for the nematodes to feed on when the beet are in the seedling stage and most vulnerable. Over what distance sugar beet roots attract nematodes is unknown, but *T. viruliferus* were attracted to roots of apple from at least 8 cm (Pitcher, 1967). That *L. elongatus* are attracted by roots of beet and other plants in Fen peat soils was shown by the extent to which they were aggregated around root tips (Whitehead & Hooper, 1970). Also, *L. attenuatus* were more abundant around the roots of both seedling and mature beet when widely spaced than when at close spacing (Table 4) (Cooke, 1968).

TABLE 4

Number of Longidorus *in soil close to sugar beet plants at different spacings, Herringswell, W. Suffolk, 1967*

Samples on 30 May		Samples on 20 October	
Seedling spacing (inches)	*Longidorus*/litre soil	Plant spacing (inches)	*Longidorus*/litre soil
6·1	296	14·2	55
2·5	286	11·2	67
1·4	198	10·4	34
0·4	180	9·5	31

Soil conditions will affect the ease with which the nematodes can move to root tips; they do so more readily in light than heavy soils and in moist than in dry soils. Seedlings have fewer roots than older plant and are less able to withstand attack. Hence, with a given population of nematodes damage is greatest in sandy soils that are weed free, drilled to a stand and are wet when the seedlings are small.

Factors affecting yield loss

Although sugar beet seedlings whose roots are damaged by *Trichodorus* or *Longidorus* are usually smaller than those that are not, there is no close relationship between nematode numbers and yield losses in different fields and years. The importance of root damage depends less on the species and abundance of the nematodes than on the time when the roots are attacked and the vigour of the seedlings, both of which are influenced by type, structure, moisture and nutrient content of the soil.

Soil. Pizer (1954) stated that there was little organic matter in the soils of affected fields, Gates (1954) found Docking disorder worst in areas of light soil with least organic matter and Gibbs (1959) recorded that it occurred in the same patches every year. Brenchley (1968), who photographed affected patches from the air, found that the disorder was often associated with changes in soil structure and texture and almost entirely confined to drift soils. Severe effects were frequently associated with areas of poor soil structure, seemingly the result of solifluxion or cryoturbation in periglacial conditions, and he thought the poor structured areas provided a favourable environment for the nematodes as well as being sometimes directly responsible for poor growth. Similar, irregular, diffuse patches of stunted beet occur on the soils derived from Bunter sandstones in Nottinghamshire and the West Midlands, and on the wind-deposited sands of Lincolnshire and Yorkshire. Table 5 gives analyses of soils from some fields where nematode infestations have caused stunting and where some of our trials have been made.

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TABLE 5

Mechanical analysis, organic matter content and pH of soil from parts of fields with Docking disorder

Site	Coarse sand (2000–200 μ) %	Fine sand (200–20 μ) %	Silt (20–2 μ) %	Clay (<2 μ) %	Organic matter %	pH (1 g soil in 2·5 ml water)
Docking, Norfolk	67	24	3	6	0·7	7·2
Gayton, Norfolk	60	27	3	9	1·2	8·2
Stoke Ferry, Norfolk	24	18	14	44	43	5·3
Herringswell, W. Suffolk	31	60	2	6	0·9	7·7
Thornton, E. Yorkshire	57	33	3	5	1·8	7·5

Soil from the worst affected patches usually contains less than 10% of clay and more than 80% of coarse fractions (fine and coarse sand). Nematodes also occur in better soils but here they are less damaging: for example, in the peat soils of Methwold Fen, near Stoke Ferry, Norfolk, *L. elongatus* is abundant and stunted sugar beet seedlings in 1969 (Whitehead & Hooper, 1970), producing typical Docking disorder symptoms, but the crop recovered and yielded satisfactorily.

Jones, Larbey and Parrott (1969) suggested that the abundance and activity of nematodes in a soil depended on their dimensions in relation to the cross section and configuration of soil spaces. Whereas root endoparasites such as *Heterodera*, which soon become sedentary inside the roots, can be plentiful in both fine and coarse soil, *Longidorus* and *Trichodorus* are abundant only in coarse soils. When prepared as seed-beds these soils provide a favourable environment for *Longidorus* and *Trichodorus* and, if the soil is excessively loose, beet can be severely damaged; sugar beet seedlings often grow better in tractor 'wheelings' than elsewhere, possibly because the nematodes move less readily through partly compacted soil. However, the effects of compaction are complex, and severe compaction or slaking of these soils can be damaging by physically restricting root growth or by making the soil nearly anaerobic. Heavier sandy soils that are compacted, perhaps by untimely cultivation, sometimes produce shallow, fangy roots and stunted, nutrient-deficient tops reminiscent of Docking disorder.

Marl applied to Norfolk light land during the 17th, 18th and 19th centuries (Fussell, 1959; Prince, 1964) has now leached from the top soil. Marling makes the soil more stable, helps root growth and decreases wind erosion; it has been done recently in sandy fields in E. Yorkshire (Park, Brown & Wright, 1970).

Rainfall. Hull (1960) observed that Docking disorder is most severe after wet springs, and Jones *et al.* correlated April–June rainfall with the acreage of beet stunted in the Cantley, Bury St. Edmunds, King's Lynn and Wissington sugar factory areas. They ranked the severity of Docking disorder at the end of June as 1967 (most), 1964, 1965, 1968, 1966 (least); 1967 was exceptionally wet in April–June and 1966 was drier than average. This ranking accorded well with the weekly cumulative rainfall during the last three weeks of May; the ranks accorded poorly with rainfall earlier and with rainfall later the accord was lost. Rainfall is the main factor affecting moisture tension in coarse, free-draining soils. The moisture tension favouring nematode movement is in the range 0·1–0·25 atm., i.e., 100–250 cm water (Wallace, 1963). Jones *et al.* suggested that the summation of ectoparasitic nematode activity during spring was proportional to cumulative rainfall, and that May rainfall determined the severity of stunting; rainfall had less

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influence after dry spells in May or early June because such spells prevent nematodes from moving and feeding and allow plant roots to extend undamaged.

In 1969 a greater area was reported affected by Docking disorder than ever before, in the factory areas considered by Jones *et al.* three times that reported in 1967; rainfall for May 1969 was slightly less than in 1967, but June was wetter. In the same areas in 1970 only 40 acres were estimated to be affected (Table 2); May and June were exceptionally dry. Frequent rain not only increases nematode activity but also leaches nitrogen from the root zone (Draycott & Last, 1971) leaches herbicides from the soil surface into the root zone and slakes and compacts the soil. These other effects alone do not produce Docking disorder, but often add to the damage done by nematodes.

Nutrients. Soils prone to producing Docking disorder contain little available mineral nitrogen, usually only about 0·05 ppm or even less (P. J. Last, *personal communication*) and little magnesium (Pizer, 1954). Nitrogen leaches readily from soils with little clay and loss is greatest during wet springs, which also favour nematode activity and root damage. The seedlings cannot then get enough nutrients from the surface soil and consequently show the signs of nitrogen and magnesium deficiency characteristic of Docking disorder.

Control of Docking disorder

Killing the nematodes in the soil is the only reliable way of preventing Docking disorder, but the damage can be ameliorated in various ways, some of which are:

A. Minimise the effects of nematode feeding.

- (i) Avoid practices that might weaken plant growth, such as
  - (a) sowing too deep or too early,
  - (b) applying too much herbicide,
  - (c) harming soil structure.
- (ii) Adopt all practices that encourage plant growth, such as
  - (a) controlling damage from other pests or diseases and from soil blowing,
  - (b) applying organic matter,
  - (c) applying extra nitrogen.

B. Minimise the amount of nematode feeding.

- (i) Provide alternative or additional feeding area, by
  - (a) inter-row cropping,
  - (b) sowing sugar beet seeds closer together.
- (ii) Limiting nematode movement, by
  - (a) marl, which also has soil-stabilising and some nutrient benefits,
  - (b) a firm seedbed.
- (iii) Kill the nematodes or repel them from the roots.

Evidence of the value of some of these practices has been reviewed above, and that for the use of additional nutrients or nematicides is given below.

Nutrients. Much of the yield loss from Docking disorder is because damaged roots do not absorb enough nutrients, and some of this loss can be partly compensated for by giving extra nitrogen to the seedbed or as a top dressing. Large dressings of seedbed

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nitrogen sometimes enable seedlings to recover from early nematode attack and produce roots of better shape and larger yield.

In several field trials from 1948 to 1954 magnesium applied as kieserite at 4–5 cwt/acre did not improve growth, whereas nitrogen in various forms often did (Shotton, 1958). In one trial, plots given 8 cwt 'shoddy' (wool waste) plus 2 cwt 'Nitrochalk'/acre yielded 12 tons roots/acre whereas those given the equivalent amount of nitrogen as sulphate of ammonia (4 cwt/acre) yielded only 5 tons/acre. In the same field in 1956, when stunting was again severe, root yield was increased from 3 tons/acre with inorganic fertiliser only, to around 10 tons/acre with 'hoof and horn' or 'shoddy' (amounts used not specified) (Shotton, 1958); presumably the benefit arose from the slow release of nitrogen from the organic fertilisers.

Of several granular fertilisers placed in the root zone of severely stunted plants in June 1965 only nitrogen increased yields (Dunning, Heathcote, Winder & Tinker, 1966), and solutions of nitrogen sometimes improved yields when similarly placed (Dunning & Winder, 1969b). In a trial at Thornton, Yorkshire, where all beet were given 1·2 cwt/nitrogen/acre in the seedbed, an extra 1 cwt of nitrogen/acre added to the seedbed increased sugar yield from 12·7 to 23·9* cwt/acre and improved root shape; when applied as a top dressing it increased yield similarly without improving root shape (Dunning & Winder, 1967).

The effect of 0, 0·66, 1·32 and 1·98 cwt nitrogen/acre applied in the seedbed as 'Nitrochalk' was tested at 15 sites between 1967 and 1969 (Draycott & Cooke, 1968, 1969; Cooke & Draycott, 1970).

In 1967 at Messingham, Lincolnshire, where *Trichodorus* was abundant, roots were badly damaged and yield was small, the largest dressing of nitrogen most improved root shape and sugar yield; at Herringswell, Suffolk, on a similar soil in the same year, where nematodes were few, root systems were normal and yield was average, the three amounts of nitrogen gave equal yield increases (Table 6). In no trial did top dressing with 0·66 cwt nitrogen/acre in June improve root shape; on average the best root shape and sugar yield were from plots given 1·98 cwt nitrogen/acre in the seedbed, which is almost twice the nationally recommended amount. In four of the 15 trials, nitrogen applied in a slow release form, as isobutyridene diurea, gave better yields than the equivalent amount as 'Nitrochalk'.

TABLE 6

Effect of nitrogen applied to the seedbed on root fanginess and sugar yield at sites with and without Docking disorder, 1967

Nitrogen applied cwt/acre	Messingham, Lincs[1]		Herringswell, W. Suffolk[2]	
	Root fanginess (0–5)†	Sugar yield (cwt/acre)	Root fanginess (0–5)†	Sugar yield (cwt/acre)
0	2·4	33·5	0·5	43·9
0·66	2·3	38·6	0·5	64·8***
1·32	2·1	48·3**	0·4	65·8***
1·98	1·7**	53·8***	0·5	63·5***

[1] *Trichodorus* spp. (mainly *T. primitivus* and *T. pachydermus*), 1750/litre of soil in April: crop affected by Docking disorder.

[2] *Longidorus attenuatus*, 10/litre of soil in April: crop not apparently affected by Docking disorder.

† 0–5 = scale of increasing root fanginess.

*, **, *** Statistically significant root shape improvement, or yield increases, at 5%, 1% and 0·1% levels of probability respectively.

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Plate 1A. Field of sugar beet with Docking disorder.

Plate 1B. Effect of tractor wheelings in field of sugar beet with Docking disorder.

Photos: Broom's Barn Experimental Station

[*facing p.* 228]

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Plate 2B. Enlarged view of rootlets injured by *Trichodorus teres*.

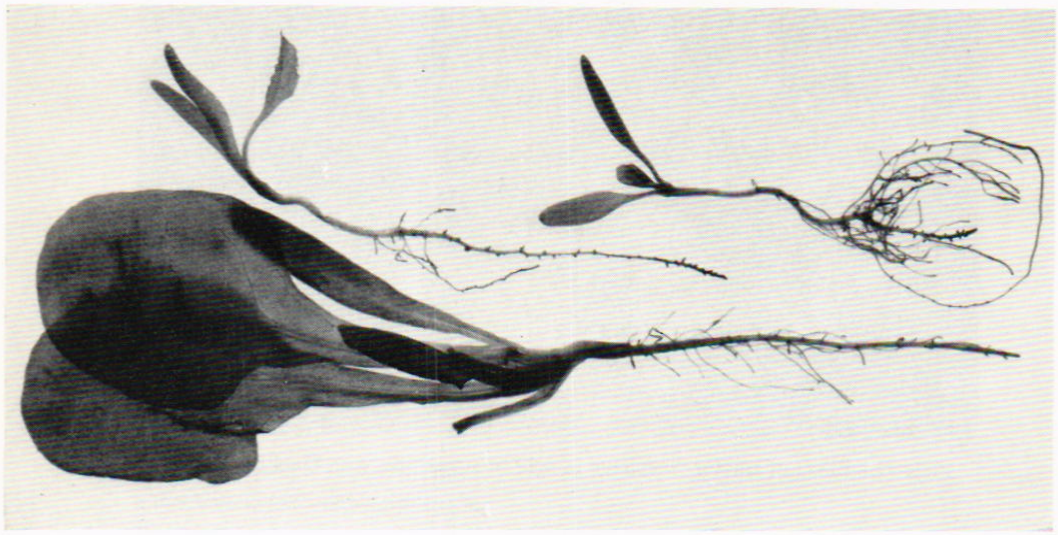

Plate 2A. Healthy sugar beet seedling (left) compared with seedlings injured by *Trichodorus teres* (right).

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Plate 2C. Sugar beet seedlings from field infested with *Longidorus elongatus*. Three very injured seedlings (left), one less injured seedling (centre) and one healthy seedling (right).

Plate 2D. Enlarged view of rootlets injured by *Longidorus elongatus*.

Photos: C.C. Doncaster

Plate 3A. Plot fumigated with 'D-D' (400 lb/acre) in sugar beet field with Docking disorder.

Plate 3B. Effect of a granular nematicide applied in the seed furrow at sowing (left) compared with an untreated row (right).

Photos: Broom's Barn Experimental Station

The results of these and other experiments (Whitehead, Tite & Fraser, 1970) show that increasing nitrogen fertiliser can increase yield, especially when in slow release form or when the supply is maintained in the surface soil by top dressing, but is not a reliable method of preventing Docking disorder.

Nematicides. *Longidorus* and *Trichodorus* feed on many different species of plants and can survive long periods in the soil without host plants, so neither changing crops nor fallowing land will greatly decrease populations, which can be done only with nematicides. Nematicides have been tested on sites prone to Docking disorder since 1955, but only since 1964 has nematode control been measured.

Overall treatment with fumigant nematicides. 'D-D' soil fumigant (1,3 dichloropropene-1,2 dichloropropane mixture) was first tested by Eastern Region, N.A.A.S., at Docking in 1955, where it and ethylene dibromide greatly improved the growth of sugar beet. In two fields, where Docking disorder occurred in 1958, injecting with 'D-D' during autumn 1957 greatly increased yields and gave less fangy roots. At 'Washpit Breck', Docking, also, 'D-D' applied during the autumn of 1955 increased the yield of sugar beet grown in 1958 from 4 to 13 tons/acre and decreased the percentage of fangy roots from 85 to 26 (Shotton, 1958). 'D-D' was not tested again until Docking disorder was attributed to ectoparasitic nematodes (Whitehead & Cooke, 1965).

Heathcote, Greet and Whitehead (1966) showed that, in 1964 in two fields prone to Docking disorder, 33·5 gal 'D-D' or chloropicrin/acre injected into the soil in December 1963 killed many nematodes, including *L. attenuatus*, and greatly increased the yield of sugar beet. 'D-D' or chloropicrin point-injected 6 inches deep at 12-inch centres (33·5 gal/acre) into sandy soil in February 1965 killed more than 95% of the *L. attenuatus* down to 20 inches. *Trichodorus* are also killed by large doses of 'D-D'. At Gayton and Santon Downham in Norfolk, fumigating the soil in this way early in 1965 with 'D-D' or chloropicrin gave good crops of sugar beet taken in 1965, 1966 and 1967 (Table 7) (Whitehead, Fraser & Greet, 1970).

TABLE 7

Effect of fumigating soil during winter 1965 on yield of sugar (cwt/acre)

Fumigation treatment	Gayton, Norfolk			Santon Downham, Norfolk	
	1965	1966	1967	1965	1966
Untreated	47·9	52·3	36·9	39·3	56·6
'D-D', 33·5 gal/acre at 12-inch centres overall	65·7***	60·9	52·4***	56·7*	74·3***
Chloropicrin, 33·5 gal/acre at 12-inch centres overall	67·8***	57·2	49·9***	64·0**	62·3

*, **, *** Statistically significant yield increases at 5%, 1% and 0·1% levels of probability respectively.

At Thornton, Yorkshire, where untreated soil had 6000 *T. anemones*/litre in April 1967, 17 gal 'D-D'/acre injected 6 inches deep at points 12 inches apart during January 1967 increased sugar yield from 27 to 53*** cwt/acre (Dunning & Winder, 1968). As little as 10 gal 'D-D', 'Telone' (mostly 1,3 dichloropropene) or ethylene dibromide/acre trickled onto the furrow bottom while ploughing during early autumn, killed 75% or more of

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Trichodorus and *Longidorus*. In one trial, 11 gal 'D-D'/acre increased sugar yield from 24·3 to 40·9* cwt/acre. Table 8 gives the results of other trials, in one of which 6 gal 'D-D'/acre increased sugar yield as much as did 24 gal/acre.

Applying soil fumigants deeper than 6 inches on the furrow bottom during late autumn or winter was much less effective, probably because the fumigants penetrated the deeper (warmer) layers of the soil rather than the surface (colder) layers; treating very wet soils was also ineffective (Whitehead & Tite, 1968; Whitehead, Tite & Fraser, 1970).

TABLE 8

Effect of small doses of fumigant applied to the furrow bottom during ploughing in autumn or winter on sugar yield of beet crops sown the next spring

Site	Fumigation treatment	Sugar yield (cwt/acre)
Docking, Norfolk	Untreated	29·3
	Ethylene dibromide, 10 gal/acre	42·0**
	Untreated	23·3
	'D-D', 10 gal/acre	31·9*
	'D-D', 20 gal/acre	35·0**
Gayton Thorpe, Norfolk	Untreated	44·4
	'D-D', 6 gal/acre	53·1**
	'D-D', 12 gal/acre	55·0**
	'D-D', 24 gal/acre	52·3**

*, **, Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

'D-D', 'Telone', ethylene dibromide, chloropicrin and other soil fumigants inhibit the bacteria that convert ammonium to nitrate, and thus retard the nitrification of ammonium nitrogen formed by mineralisation of soil organic nitrogen or added as fertiliser. Fumigation can also cause a flush of mineralisation of soil organic nitrogen (Gasser & Peachey, 1964). Hence, after fumigation, more of the mineral nitrogen in the soil is in the ammonium form, which is adsorbed onto the clay particles and humus, and less is in the more readily leached nitrate form. Also the total amount of mineral nitrogen in the soil may be increased.

At Herringswell, Suffolk, 33·5 gal 'D-D'/acre injected at points 12 inches apart during December 1965, slowed nitrification and thus decreased leaching, but did not increase the total amount of mineral nitrogen in the soil profile down to 24 inches next May. Ninety-seven per cent of the plant parasitic nematodes in the soil were killed, and the yields of sugar beet, barley, ryegrass and potatoes were greatly increased. In 1968 unfumigated plots and plots fumigated in 1965 or 1966 contained similar amounts of mineral nitrogen, similarly distributed through the soil profile, but those fumigated in 1967 had more mineral nitrogen, especially in soil down to 4·5 inches. Docking disorder was not apparent in any plot, but all fumigated plots contained few *L. attenuatus* and yielded more sugar than unfumigated plots (Table 9); this suggests that most of the yield increase was from killing nematodes, not from increasing soil nitrogen (Cooke, Draycott & Hull, 1969).

In 15 trials in 1967–69 less nitrogen fertiliser was needed on average to achieve optimum yield after fumigation with 33·5 gal 'D-D'/acre, partly because 'D-D' increased the amount of mineral nitrogen in the surface soil and partly because root systems were not damaged by nematodes and were therefore better able to absorb nutrients (Table 10) (Draycott & Cooke, 1968, 1969; Cooke & Draycott, 1970).

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TABLE 9

Mineral nitrogen measured in the soil, numbers of L. attenuatus *and sugar yield in 1968 after fumigation treatments in 1965–67 at Herringswell, W. Suffolk*

Fumigation treatment		Mineral nitrogen (lb/acre)	*L. attenuatus* (no./litre soil)	Sugar yield (cwt/acre)
Untreated		126	110·8	65·1
'D-D', 33·5 gal/acre at 12-inch centres overall	in 1965	119	9·8	74·9
'D-D', 33·5 gal/acre at 12-inch centres overall	in 1966	117	4·4	75·4
'D-D', 33·5 gal/acre at 12-inch centres overall	in 1967	162	0·3	76·9

TABLE 10

Mean effects of nitrogen applied to the seed bed and fumigating the soil in winter, on sugar yield at 15 sites, 1967–69

Fumigation treatment	Nitrogen applied to seedbed (cwt/acre)			
	0	0·66	1·32	1·98
	Sugar yield (cwt/acre)			
Untreated	33·7	41·9	44·8	46·2
'D-D', 33·5 gal/acre at 12-inch centres overall	49·4	58·3	58·2	58·3

Least significant difference between any two treatment means—4·6, 6·1 and 7·9 at 5%, 1% and 0·1% levels of probability respectively.

Row treatment with small amounts of fumigant. As sugar beet is a row crop (row width 21 inches on average) and Docking disorder is principally a seedling problem, our more recent work has concentrated on treating the rows with fumigant or systemic nematicides. This is cheaper than treating the whole field and enables the beet seedlings to develop a good primary root system and to grow vigorously. Once the plants are well established, attack by nematodes from the soil between the rows seems not to be damaging.

'D-D' injected during January 1965, 6 inches deep at points 12 inches apart in all directions, was compared with 'D-D' injected 6 inches deep at points 12 inches apart along the lines of the predetermined sugar beet rows, spaced 21 inches apart. All treatments increased sugar yield in 1965, more from injections of 13·5 or 19 gal/acre along the rows than from 38 gal along the rows or 24 or 33·5 gal injected at points 12 inches

TABLE 11

Yield of sugar and of barley grain at Gayton, Norfolk, in 1965–67 after two methods of fumigation in January 1965

Fumigation treatment	Yields (cwt/acre)		
	Sugar 1965	Barley grain 1966	Sugar 1967
Untreated	52·3	26·9	39·7
'D-D', 13·5 gal/acre at 12-inch centres in rows 21 inches apart	64·2***	31·1**	50·9***
'D-D', 19 gal/acre at 12-inch centres in rows 21 inches apart	61·5**	30·4**	54·2***
'D-D', 38 gal/acre at 12-inch centres in rows 21 inches apart	56·6	30·5**	54·1***
'D-D', 24 gal/acre at 12-inch centres overall	56·2	30·0*	51·4***
'D-D', 33·5 gal/acre at 12-inch centres overall	57·0	31·0**	51·4***

*, **, *** Statistically significant yield increases at 5%, 1% and 0·1% levels of probability respectively.

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apart, probably because the larger amounts damaged plant growth. The tops and roots were removed from all plots; all fumigation treatments gave similar grain yield increases in barley sown in 1966. Sugar beet was grown in 1967, when again there were large benefits from the 'D-D' applied by either method in 1965 (Table 11) (Whitehead, Tite & Fraser, 1970).

'D-D' applied 10 inches deep on the furrow bottom during ploughing in early November 1966 in rows 18 inches apart and marked at intervals of 12 ft by sowing winter wheat, so that sugar-beet rows could be drilled in the fumigated bands next spring (Whitehead & Tite, 1968), killed few *T. cylindricus* in the top 8 inches of soil but many in the layer 12–20 inches deep. Sugar yield was increased from 23·1 to 42·7** cwt/acre by applying 9 gal 'D-D'/acre in this way, but 4·5 gal had much less effect and 2 gal had none. 'D-D' applied in rows by 'plough-sole' (i.e. as above) or 'knife-coulter' methods in September 1967 increased sugar yields in 1968 (Table 12) (Whitehead & Tite, 1969).

TABLE 12

Yield of sugar at Docking, Norfolk, 1968, after fumigating the rows during September 1967

Fumigation treatment (continuous flow in rows 18 inches apart)	Yield of sugar (cwt/acre)	
	'Plough-sole' application	'Knife-coulter' application
Untreated	28·9	34·4
'D-D', 6·5 gal/acre	38·6*	35·9
'D-D', 13·0 gal/acre	40·8**	41·2*

*, ** Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

Row fumigation during spring shortly before drilling is an accepted practice in parts of the U.S.A. for some field crops, but the soil in England had been thought to be too cold during March and April for the fumigant to disperse before sugar beet seeds germinate. However, in an experiment at Docking in 1967, 4, 8 and 16 gal 'Telone'/acre trickled 10 inches deep close to sugar beet rows immediately after sowing killed many *T. cylindricus* in the rows and increased sugar yields from 22·1 to respectively 45·9***, 40·4** and 35·1* cwt sugar/acre. Trials at Docking in 1968 tested different amounts of 'D-D' and 'Telone' injected 3, 6 and 9 inches deep by knife-coulters in the predetermined beet rows three weeks before sowing (Whitehead & Tite, 1969). Yield increases were greatest from the 6-inch and 9-inch treatments, but Table 13 gives results averaged over the three depths.

These experiments showed that as little as 6 gal 'D-D' or 4 gal 'Telone'/acre injected beneath the rows at or before drilling could control *L. attenuatus* and *Trichodorus* spp. well enough to allow the seedlings to grow normally. In 1969, 6 gal 'D-D'/acre, injected by knife-coulters 6–8 inches deep along the rows two weeks before sowing, killed 84% of *T. cylindricus* at one site and 91% of *L. attenuatus* at another in the rows, but only 25% and 68% respectively 5 inches from the rows, and none 10 inches from the rows (Cooke, Dunning & Winder, 1970).

Row fumigation during spring is commercially practical and was successful at Ripper Farms Ltd., Docking, in 1968 and 1969. In rows thus treated with 6·4 gal 'D-D'/acre two to three weeks before sowing in 1968, 85% of *T. cylindricus* were killed, and seedlings growing in the rows in June weighed more than ten times as much as seedlings in untreated

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TABLE 13

Effect on sugar yield of fumigating the rows three weeks before sowing at Docking, Norfolk, 1968

Fumigation treatment (continuous flow in rows 18 inches apart)	Sugar yield (cwt/acre)
Untreated	40·2
'D-D', 4 gal/acre	46·6*
'D-D', 8 gal/acre	48·2*
Untreated	39·4
'Telone', 4 gal/acre	45·8
'Telone', 8 gal/acre	49·8**

*, ** Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

rows; treated rows yielded 18 cwt/acre more sugar than untreated rows (Whitehead & Tite, 1969). Seedlings from rows similarly treated in 1969 with 6·4, 9·6 or 12·8 gal 'D-D'/acre weighed ten to 20 times more than seedlings from untreated rows; rows treated with 6·4 gal/acre yielded 12 cwt more sugar/acre than untreated rows (Whitehead, Tite & Fraser, 1970). In 1970 some 1000 acres were treated commercially with 'D-D' or 'Telone', mainly in East Anglia.

Row treatment with small amounts of systemic nematicide. At Hopton and Swaffham, Norfolk, in 1964, sugar yield was increased or fanginess of roots was decreased by granules containing dibromochloropropane, phorate or thionazin, applied at 4–22 oz a.i./acre in the seed furrow. These results first indicated that very small amounts of pesticide placed close to sugar beet seeds could lessen losses from Docking disorder (Dunning & Winder, 1969b). In 1966 menazon seed dressing, and in 1967 thionazin and phorate granules in the seed furrow, improved the shape and yield of sugar beet roots in soil infested with *T. anemones* at Thornton, Yorkshire, but in other fields thionazin and phorate damaged the beet and menazon was ineffective.

Of 29 pesticides tested by applying small amounts in the seed furrow at sowing in 1967, 1968 and 1969, aldicarb ('Temik') controlled Docking disorder best. Small amounts

TABLE 14

Effect of systemic nematicides applied with the seed on root fanginess and sugar yield

	Thornton, E. Yorkshire			Hellesdon, Norfolk		
Systemic nematicide treatment	oz a.i./acre	Root fanginess‖ (0–5 scale)	Sugar yield (cwt/acre)	oz a.i./acre	Root fanginess‖ (0–5 scale)	Sugar yield (cwt/acre)
Untreated	—	3·1	29·2	—	1·8	48·5
Thionazin granules	9	2·9	45·8***	9	1·4	51·9
Aldicarb granules	16	0·7***	62·2***	7	0·7***	80·2***
,, ,,	7	0·8***	53·7***	5	0·5***	77·4***
,, ,,	4	1·0***	55·8***	2	0·5***	76·9***
Methomyl solution	40	2·1***	21·6	48	1·2**	64·2*
,, ,,	13	2·0***	38·5*	16	0·7***	71·9***
,, ,,	4	2·6*	40·4*	5	0·4***	70·4**

‖ 0–5 = scale of increasing root fanginess.
*, **, *** Statistically significant improvement in root shape or sugar yield at 5%, 1% and 0·1% levels of probability respectively.

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of methomyl ('Lannate') solution also greatly increased sugar yields in two trials in 1967 (Table 14) but damaged beet in 1968 and 1969. The 1967 trials were with single-row plots, so the yield increases in Table 14 are somewhat exaggerated.

At Docking in 1967, where the soil was infested with *T. cylindricus*, 48 oz methomyl/acre, sprayed in a 6-inch wide band over the sugar beet rows immediately after sowing, increased sugar yield from 22·1 to 43·1*** cwt/acre (Whitehead, Tite & Fraser, 1970).

Aldicarb granules were applied in the seed furrows at ten sites in 1968 and at nine in 1969; Docking disorder occurred at three in 1968 and all nine in 1969. Averaging all 19 trials, 4, 8 and 16 oz a.i./acre increased yield from 48·9 cwt sugar/acre to 52·3, 53·2 and 54·4 cwt sugar/acre; at the current price of aldicarb its use was justified only at the sites where Docking disorder was severe (Dunning & Winder, 1970). Aldicarb seems not very toxic to *T. anemones*, for treating soil with as much as 100 ppm decreased numbers extracted by only 67% after three weeks (Dunning & Winder, 1969a). However, it seems to prevent the nematodes feeding on roots that have absorbed it from the soil, and this is enough to make seedlings grow more vigorously.

Aldicarb is a strong cholinesterase inhibitor and is therefore hazardous to apply, but small amounts can conveniently be applied at sowing with a granule applicator mounted on the seed drill. Aldicarb thus applied also protects the seedlings from beet leaf miner (*Pegomya betae* (Curt.)) and aphids, and checks the spread of 'virus yellows' virus (Dunning & Winder, 1969a).

Four field trials in 1969 compared 6 gal 'D-D' or 'Telone'/acre, applied 6–8 inches deep in the rows two weeks before or immediately before sowing, with 8 oz a.i. aldicarb/acre applied as granules in the seed furrow during sowing. The average sugar yield from the untreated plots was 50·0 cwt/acre; 'Telone' injected two weeks before sowing or immediately before sowing increased yield to 58·8 and 57·9 cwt/acre respectively, 'D-D' (both times of application) to 57·5 cwt/acre and aldicarb granules to 54·9 cwt/acre. Aldicarb was probably less effective because nitrogen was leached by the excessive rain in May (Cooke, Dunning & Winder, 1970).

Summary

Ectoparasitic nematodes, especially species of *Trichodorus* (stubby root nematodes) and *Longidorus* (needle nematodes), feed on and damage the root tips of sugar beet; Docking disorder is the poor growth of sugar beet resulting from this primary damage. Yield loss does not depend only on the number of nematodes in the soil, but also on other interacting factors, especially soil structure and rainfall, which affect the numbers and activity of the nematodes, the nutrients available to the seedlings and the vigour of root growth. Modern cultural practices, especially the use of herbicides and drilling to a stand probably increase the prevalence and severity of Docking disorder. Approximately 20 000 acres of sugar beet suffered from Docking disorder in 1969, at an estimated yield loss exceeding 50 000 tons of roots.

Damage can be alleviated by correct use of nitrogen, principally by avoiding leaching or replacing the nitrogen lost by leaching, and it can be prevented by nematicides. Fumigating all the top soil with 'D-D' or 'Telone' kills nearly all the nematodes and greatly increases the yield of sugar beet and other crops in the rotation, but is expensive. Small amounts of fumigant or systemic nematicides applied to the sugar beet rows at or before sowing kill most of the nematodes in the rows, or prevent them from feeding on the roots, allow the seedlings to grow vigorously, and can greatly increase yield.

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Rothamsted Insect Survey

L. R. TAYLOR and R. A. FRENCH

Suction traps

New traps operated, in England, at N.A.A.S. South-West Region Sub-Centre, Starcross, near Exmouth, Devon; at the University of Bristol, Research Station, Long Ashton, near Bristol; at the Building Research Station, Garston, Watford, Hertfordshire; in Scotland, at the North of Scotland College of Agriculture Experimental Farm, Aldroughty, near Elgin, Inverness-shire.

Weekly bulletins listing catches of 31 aphid species, or groups of species, from 13 traps were issued from 4 May to 8 November. The list of species was revised slightly from last season; *Aphis fabae* group was retained but other *Aphis* spp. were grouped together because of uncertainty in their separation; *Pentatrichopus fragaefolii* was omitted because it was rarely caught. From 25 June to 5 August the volume of air sampled by the traps at Wye, Silwood Park, Long Ashton, Rothamsted and Brooms Barn was halved and from 1 October to 28 October it was halved on all traps. This eased the heavy sorting and identifying during these peak periods and helped the bulletin to be issued on time. Tables 1a–g have been adjusted to give the expected catch in a standard sample of air.

Because of the warm spring weather aphid populations developed rapidly and migration reached its first peak one to two weeks earlier than in previous years but did not exceed previous years' totals.

The original trap at Rothamsted was replaced at the beginning of this season and the trap at Dundee will need replacing before next season; that at High Mowthorpe requires repair. The fans and motors can be used again. The life expectancy of the earlier traps is thus five to six years but it is hoped that improvements made since will result in traps lasting ten years.

The West-East transect has not yet been expanded beyond Zeeland (Holland). The only immediate further extension of the survey envisaged for purely experimental purposes is to offshore islands, but some increase in the centre of England may be warranted by both the need for replication and the demand for traps in regions where N.A.A.S. officers can most effectively assess their advisory value. It is expected that as last year, traps will have detected the first immigrants into cereals before they were found by crop sampling.

Table 1a–g lists the same 31 taxa as those in the weekly bulletins in the same four-week standard periods as in 1969. The Garston and Aldroughty traps are not included because they did not operate for a complete season. Traps are arranged in a north to south sequence; blanks in the table are zero catches; there are no missing records.

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Light traps

Tables 2a–d give total annual catches for 31 species of nocturnal Lepidoptera, including some known migrants and species of economic importance. The 60 sites that completed the 1969 year are arranged in north to south sequence; dashes indicate missing records from traps not operating in 1968 and for those sites from which the Microlepidoptera are not identified. We are again deeply indebted to the many voluntary workers who operate traps and identify catches during their spare time.

TABLE 2 *The Rothamsted Insect Survey—Light Traps* is on pages 246–253.

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TABLE 1(a)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 17–20: 23 April–20 May

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum								2	3	2	1		
Aphis fabae									1				
Aphis spp.													
Amphorophora spp.													
Aulacorthum solani								2				1	1
Brachycaudus helichrysi								1	1			2	6
Brevicoryne brassicae													
Cavariella aegopodii									1			1	
Cinara spp.						1							
Drepanosiphum platanoidis				2	157	871	113	588	1292		389	56	
Dysaphis plantaginea													
Elatobium abietinum					5			4	3		1	1	4
Eriosoma ulmi													
Hyalopterus pruni													
Hyperomyzus lactucae									2				
Macrosiphum euphorbiae								1	1			1	
Megoura viciae													
Metapolophium dirhodum								2	2	2	1	1	
Metapolophium festucae						1		40	1			1	1
Myzus ascalonicus			1			13	9	18	9	3	3	5	9
Myzus ornatus					1			4	2			1	1
Myzus persicae						1		2	1			2	
Nasonovia ribis nigri								4	4			2	
Pemphigus spp. / *Prociphilines*													
Phyllaphis fagi						2	1		1				
Phorodon humuli													
Rhopalosiphum insertum													1
Rhopalosiphum maidis													
Rhopalosiphum padi					1	3		1	5			3	
Sitobion avenae								2	2			1	2
Sitobion fragariae					1			1	1			2	
First aphid caught			May 19	May 18	May 12	May 10	May 8	May 7	May 4	May 7	May 9	May 5	May 7

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TABLE 1(b)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 21–24: 21 May–17 June

Species	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum	1			4	17	30	53	17	21	30	9	8	2
Aphis fabae		1		2	1		1	15	11		20	6	4
Aphis spp.	1				6	4	12	63	55	1	31	10	2
Amphorophora spp.					3		1	19	3		12	1	2
Aulacorthum solani					10	2		14	2		1	5	32
Brachycaudus helichrysi	7	10	3	25	1914	105	145	986	306	8	435	226	934
Brevicoryne brassicae						49	6		2	1		9	3
Cavariella aegopodii		6	1	7	50	16	10	168	52	44	34	34	24
Cinara spp.					1			5	4	1	3		1
Drepanosiphum platanoidis	417	893	720	5310	1804	672	1571	160	1255	1	448	160	7
Dysaphis plantaginea						3	2	13	24			8	
Elatobium abietinum	4	3	12	2	294	2	6	10	44		64	11	2
Eriosoma ulmi		1		1	19	259	192	237	396	87	103	8	
Hyalopterus pruni	4				13	2	8	47	60	8	7	14	4
Hyperomyzus lactucae	2	10		1	27	8	6	74	29		36	5	5
Macrosiphum euphorbiae	1	2			8	1	4	24	17	1	9	14	7
Megoura viciae								5	2		4		
Metapolophium dirhodum	1	1			4		8	37	46	1	8	33	12
Metapolophium festucae		1			14	2	3	57	27		7	18	48
Myzus ascalonicus	2	39	3	13	16	48	262	45	47	3	62	18	19
Myzus ornatus							1	5	1		1	2	1
Myzus persicae					3	2	1	21	10	2	3	7	4
Nasonovia ribis nigri	1	2		1		3	10	20	13	2	7	4	
Pemphigus spp. / *Prociphilines*						1	4	3	96			2	1
Phyllaphis fagi			1	6	1	15	5	31	43	10	17	5	9
Phorodon humuli		1		1	144	47	16	144	118	3	353	3	2
Rhopalosiphum insertum	8	10	10	37	1	19	13	19	12	30	18	2	16
Rhopalosiphum maidis						1							2
Rhopalosiphum padi	131	159	217	545	298	340	578	227	190	12	232	27	82
Sitobion avenae					3	3	7	83	93	2	19	72	18
Sitobion fragariae		2		1	8	1	2	68	25	1	25	43	32
First aphid caught	May 22	May 23											

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TABLE 1(c)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 25–28: 18 June–15 July

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum	1	2	2	10	5	128	16	3	13	36	97	8	1
Aphis fabae	1	4	4	12	2	18	16	16	11	66	257	31	4
Aphis spp.	1	3	1	8	2	4	14	12	19	29	162	7	5
Amphorophora spp.					1						4		
Aulacorthum solani					1	8	1		1	1	1		5
Brachycaudus helichrysi	5	5	2	39	150	148	5	15	11	64	100	14	32
Brevicoryne brassicae				1		330	13		5	14	4	19	3
Cavariella aegopodii	4	20	7	23	7	7	3	40	12	250	16	4	2
Cinara spp.								4		1	1	2	
Drepanosiphum platanoidis	166	353	45	418	12	27	109	12	34	2	72	6	4
Dysaphis plantaginea						3	2	1	4	13	3	2	
Elatobium abietinum					3								
Eriosoma ulmi	58	99	17	30	10	411	116	53	33	83	83	4	2
Hyalopterus pruni	7	3	14	33	18	124	73	108	26	152	184	35	13
Hyperomyzus lactucae	4	1		2	8	3	11	8	7	30	60	8	6
Macrosiphum euphorbiae					1	10	4	10	8	2	30	48	1
Megoura viciae	1	1			3				4		3		2
Metapolophium dirhodum	18	55	9	78	3	1058	885	26	233	1181	1508	405	49
Metapolophium festucae		7	2	15	4	4	4	3	7	8	9	5	3
Myzus ascalonicus		2				3				1	4	1	
Myzus ornatus		1									1		
Myzus persicae				2	5	28	2	5	7	186	80	6	7
Nasonovia ribis nigri		2		2	5	4		7	3	3	6	4	2
Pemphigus spp. / *Prociphilines*	3	4	8	15	6	67	68	63	77	130	63	9	
Phyllaphis fagi	2	9	18	12	8	3		2	3	4	16	3	
Phorodon humuli	6	1	1	5	5	22	2	27	6	8	182	1	1
Rhopalosiphum insertum	16	9	18	189	11	34	13	13	4	50	21	5	1
Rhopalosiphum maidis		1	4		18	2		4	4	2	7	16	6
Rhopalosiphum padi	25	19	97	166	14	453	73	1	38	1086	325	56	39
Sitobion avenae	4	4	4	15	29	182	267	111	515	322	607	454	42
Sitobion fragariae		1			4	16		1	22	11	48	14	4

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TABLE 1(d)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 29–32: 16 July–12 August

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum	21	8	3	23	6	414	266	2	19	1	99		
Aphis fabae	823	62	29	1135	120	1657	1090	67	189	882	589	22	8
Aphis spp.	24	84	5	156	46	244	131	30	51	182	130	6	3
Amphorophora spp.	3												
Aulacorthum solani					1			2			2		
Brachycaudus helichrysi	35	39	4	22	56	161	22	4	4	11	12	5	1
Brevicoryne brassicae				6		2869	235	4	204	16	38	29	4
Cavariella aegopodii	20	15	6	8	1	35	7		3	32	10		1
Cinara spp.		2					1	4		1			
Drepanosiphum platanoidis	37	94	34	122	41	64	46	19	85	1	14	17	7
Dysaphis plantaginea						6							1
Elatobium abietinum													
Eriosoma ulmi		4	2	1		14	6	2	2	1	8	1	
Hyalopterus pruni	8	8	3	9	9	143	72	77	24	129	298	28	7
Hyperomyzus lactucae	12	1	3	7	4	24	20			12	4	1	
Macrosiphum euphorbiae	37	35	8	2	5	26	16	3	6	28	50	6	
Megoura viciae										1	4	1	
Metapolophium dirhodum	1299	2036	353	599	13	1827	2303	4	206	513	1212	29	11
Metapolophium festucae	7	23	1	2		16	8			1	10		
Myzus ascalonicus		1											
Myzus ornatus							1						
Myzus persicae	114	10	10	44	8	445	65	6	12	1640	141	4	1
Nasonovia ribis nigri		2	1	2		4	6			1	8		1
Pemphigus spp. / *Prociphilines*	18	11	6	11	9	162	25	10	12	27	47	6	8
Phyllaphis fagi													
Phorodon humuli	1					1				1	10		
Rhopalosiphum insertum	455	440	375	283	28	60	60	6	92	186	77	16	10
Rhopalosiphum maidis	4		1		21	5	8		2	8	3	3	3
Rhopalosiphum padi	3375	2601	1034	1040	80	3537	447	72	90	2541	1028	265	74
Sitobion avenae	141	124	176	1042	241	2694	2186	494	1611	820	1492	205	61
Sitobion fragariae	9	27		3	8	10	6		2	5	10	3	2

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TABLE 1(e)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 33–36: 13 August–9 September

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum	5	2		3	2								
Aphis fabae	609	137	29	253	13	40	23	5	8	1	1	1	1
Aphis spp.	28	52	4	40	2	8	1	14	13		5		1
Amphorophora spp.	2												
Aulacorthum solani		1											
Brachycaudus helichrysi	15	19	3	1	9	9	4	7	3		7	8	1
Brevicoryne brassicae				6	3	64	7		37	1	2	3	
Cavariella aegopodii	18	3				1			2				1
Cinara spp.													
Drepanosiphum platanoidis	97	52	5	51	119	177	66	28	230		26	25	10
Dysaphis plantaginea						1	1		3			2	
Elatobium abietinum													
Eriosoma ulmi						2			1				
Hyalopterus pruni	8	5	2	1	1	18	6	3	14	39	20	5	1
Hyperomyzus lactucae				1									
Macrosiphum euphorbiae	15	12	2		2								
Megoura viciae													
Metapolophium dirhodum	28	46	3	2									
Metapolophium festucae		2											
Myzus ascalonicus													
Myzus ornatus													
Myzus persicae	86	12	2	2	2	2			1	11	3	4	1
Nasonovia ribis nigri		1		1					2				
Pemphigus spp. }	43	36	45	7	6	13	24	18	59	6	9	6	3
Prociphilines }													
Phyllaphis fagi	1	1											
Phorodon humuli											2		
Rhopalosiphum insertum	127	69	59	23	13	3			41	11	2	5	1
Rhopalosiphum maidis	7	1			4	4							
Rhopalosiphum padi	1978	1268	184	205	26	34	5	11	15	33	27	34	4
Sitobion avenae	258	74	21	50	8	23	4	7	13	2	6	3	10
Sitobion fragariae		6		1				1					

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TABLE 1(f)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 37–40: 10 September–7 October

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum					4			2	2				1
Aphis fabae	25	70	11	4	61	5		3	6	3	6		8
Aphis spp.	19	29	4	2	22	5	7	19	25	2	12	6	2
Amphorophora spp.													
Aulacorthum solani													
Brachycaudus helichrysi	17	46	7	24	79	46	51	30	51		15	30	14
Brevicoryne brassicae			2	8	2	1	1	2	5		32	1	
Cavariella aegopodii	3	1		1	6	10		6	2		2		2
Cinara spp.		2					1		2				
Drepanosiphum platanoidis	295	150	28	143	72	32	33	30	126	4	19	20	30
Dysaphis plantaginea	1	1		3	59	2	20	36	178	1	22	33	1
Elatobium abietinum													
Eriosoma ulmi					2	1				4			
Hyalopterus pruni	11	1	4	3		12	2	8	12	46	27	8	
Hyperomyzus lactucae	1	1				2	2	4	1	2	4	10	1
Macrosiphum euphorbiae					1				1	1			
Megoura viciae													
Metapolophium dirhodum		1			3			7		1		2	
Metapolophium festucae									1			2	
Myzus ascalonicus	1											1	
Myzus ornatus								2	2				
Myzus persicae	6	1		1	14	1	3	7	2	4	27	15	2
Nasonovia ribis nigri					8			2	4			2	
Pemphigus spp. } *Prociphilines* }	154	646	89	59	162	319	90	108	101	25	69	44	17
Phyllaphis fagi		3							1				
Phorodon humuli									7	1	62		
Rhopalosiphum insertum	1229	1643	553	105	3282	6	49	111	137	16	28	375	190
Rhopalosiphum maidis	1	1	1		3			6			4	6	1
Rhopalosiphum padi	3628	6761	514	399	7213	1182	942	4703	4100	388	5010	1984	283
Sitobion avenae		4			8		1	1	1		4	2	1
Sitobion fragariae		1	1		6							3	

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TABLE 1(g)

The Rothamsted Insect Survey—Suction Traps: 4-weekly total catches of aphids of economic interest reported in the Weekly Bulletin

Week Nos 41–44: 8 October–4 November

Species \ Sites	Dundee	Edinburgh	Newcastle	High Mowthorpe	Aberystwyth	Brooms Barn	Rothamsted Tower	Long Ashton	Silwood Park	Zeeland	Wye, Kent	Starcross	Rosewarne
Acyrthosiphon pisum								2	2				
Aphis fabae		2			12	10	4	2	15	24	4	4	6
Aphis spp.			2	2	4	5	6	23	28		29	8	
Amphorophora spp.													
Aulacorthum solani					12	2					1	2	
Brachycaudus helichrysi		18	4	16		8	10	3	12	2	10	5	2
Brevicoryne brassicae				2		2			4		10	2	1
Cavariella aegopodii	2	2			2	14	7	6	8	1	5		
Cinara spp.									2				
Drepanosiphum platanoidis	106	136	80	64	53	44	41	48	60	7	40	17	22
Dysaphis plantaginea			2	1	8	8	32	24	108		158	36	10
Elatobium abietinum													
Eriosoma ulmi				2	2		2			4			1
Hyalopterus pruni				2		4	2		8	4	5		
Hyperomyzus lactucae				2	4	18	2	16	14	21	14	33	5
Macrosiphum euphorbiae										1	2		
Megoura viciae													
Metapolophium dirhodum	1	8	6		10			6	6	1	8		
Metapolophium festucae					2			1	2				
Myzus ascalonicus	2									1	4	1	
Myzus ornatus								2				2	
Myzus persicae	6	4		2	24	10	8	8	17	31	97	21	7
Nasonovia ribis nigri				4	12	4	4		2	1	6	1	3
Pemphigus spp. } *Prociphilines* }	102	162	150	40	20	358	168	435	250	24	232	119	6
Phyllaphis fagi	4	10						1	4				
Phorodon humuli								2	13		12	1	
Rhopalosiphum insertum	704	1360	1832	94	2238	132	200	259	459	77	362	338	294
Rhopalosiphum maidis		4		4	4	18		2			2	6	
Rhopalosiphum padi	1439	3438	1490	308	5661	1093	1916	10272	3136	1127	5596	3202	585
Sitobion avenae			2					6	10	1	4	10	1
Sitobion fragariae	2	4			67			41	12		2	15	16

https://doi.org/10.23637/ERADOC-1-5

TABLE

The Rothamsted Insect Survey—Light Traps: two years'

Pest Species	Year	59 Morangie	57 Ardross	58 Newton, Elgin	50 Grula, Skye	49 Fort Augustus	83 Killiecrankie (Pass)	29 Rannoch	60 Aros	48 Kindrogan	47 Dundee	82 Dunblane	97 Rowardennan	98 Auchencruive	39 Chester le Street	108 Egremont	72 Castletown, I.O.M.
Gortyna micacea Rosy Rustic	1968	—	297	104	—	82	—	145	228	—	32	97	3	18	4	—	64
	1969	226	286	124	135	96	21	79	64	238	6	138	1	17	5	36	29
Bupalus piniaria Bordered White	1968	—	0	2	—	6	—	0	0	—	0	0	0	0	0	—	0
	1969	0	0	6	0	6	0	0	0	0	0	2	0	0	0	0	0
Panolis flammea Pine Beauty	1968	—	0	5	—	9	—	4	0	—	0	0	0	0	0	—	0
	1969	0	0	1	1	5	0	1	0	0	0	0	0	0	0	0	0
Cerapteryx graminis Antler Moth	1968	—	13	29	—	194	—	78	342	—	9	35	79	13	0	—	7
	1969	51	29	47	268	317	21	121	676	240	34	336	147	31	0	8	1
Erannis aurantiaria Scarce Umber	1968	—	32	3	—	103	—	146	2	—	0	0	17	0	0	—	0
	1969	0	21	6	0	28	87	1	0	72	0	0	11	0	0	0	0
Operophtera fagata Northern Winter Moth	1968	—	6	5	—	16	—	136	0	—	1	0	22	0	0	—	0
	1969	0	0	0	0	0	8	8	0	0	0	0	8	0	0	0	0
Apamea sordens Rustic Shoulder-knot	1968	—	1	0	—	3	—	0	0	—	3	3	0	1	7	—	0
	1969	0	1	2	2	0	3	0	0	0	1	5	0	7	13	2	8
Gortyna flavago Frosted Orange	1968	—	0	4	—	0	—	0	0	—	2	0	0	0	0	—	0
	1969	0	0	2	0	0	9	0	0	1	2	0	0	0	0	2	0
Mamestra brassicae Cabbage Moth	1968	—	0	0	—	0	—	0	0	—	8	5	0	0	19	—	0
	1969	0	0	0	1	0	0	0	0	0	6	4	0	0	8	5	0
Noctua pronuba Large Yellow Underwing	1968	—	4	20	—	4	—	0	5	—	14	24	10	12	8	—	38
	1969	17	1	23	15	2	1	0	7	10	31	44	18	18	14	4	31
Diataraxia oleracea Bright-line Brown-eye	1968	—	0	13	—	0	—	0	8	—	2	2	0	6	4	—	18
	1969	6	3	11	15	0	0	0	6	0	0	3	0	5	4	11	24
Euxoa nigricans Garden Dart	1968	—	0	1	—	0	—	4	0	—	1	1	0	0	3	—	0
	1969	0	0	0	1	0	0	0	0	0	3	3	0	0	0	0	0
Apamea secalis Common Rustic	1968	—	0	100	—	22	—	0	15	—	21	40	1	68	18	—	66
	1969	3	10	58	110	3	3	0	33	1	19	85	1	60	12	33	55
Melanchra persicariae Dot Moth	1968	—	0	0	—	0	—	0	0	—	0	0	0	0	0	—	0
	1969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Operophtera brumata Winter Moth	1968	—	52	10	—	28	—	15	12	—	3	2	97	1	0	—	1
	1969	0	22	4	2	6	2	1	7	12	0	1	75	0	0	0	2

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records of the moths of economic interest (1968 and 1969)

45 Malham Tarn	40 Lancaster	68 Harrogate	101 Keighley	96 Riseholme	95 Gibraltar Point	35 Bangor	71 Rhyd y Creuau	77 Maentwrog	79 Shardlow	61 Sutton Bonington	117 Burton upon Trent	53 Preston Montford	119 Darlaston	112 Shirley	Year	Pest Species
0	7	44	—	—	—	0	—	7	30	3	—	—	—	—	1968	*Gortyna micacea*
4	5	23	52	16	109	0	42	10	24	7	23	18	0	0	1969	Rosy Rustic
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Bupalus piniaria*
0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	1969	Bordered White
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Panolis flammea*
0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1969	Pine Beauty
24	1	0	—	—	—	5	—	48	6	0	—	—	—	—	1968	*Cerapteryx graminis*
159	0	1	8	2	14	0	26	63	6	0	7	2	0	0	1969	Antler Moth
48	0	3	—	—	—	1	—	87	0	1	—	—	—	—	1968	*Erannis aurantiaria*
16	0	4	0	0	0	0	0	93	0	0	0	0	0	0	1969	Scarce Umber
18	0	0	—	—	—	0	—	105	0	0	—	—	—	—	1968	*Operophtera fagata*
3	0	0	1	0	0	0	0	62	0	0	0	0	0	0	1969	Northern Winter Moth
1	2	1	—	—	—	0	—	0	8	2	—	—	—	—	1968	*Apamea sordens*
3	0	0	0	5	18	2	0	0	0	1	0	0	13	0	1969	Rustic Shoulder-knot
0	1	2	—	—	—	0	—	0	0	2	—	—	—	—	1968	*Gortyna flavago*
0	0	3	0	1	12	0	2	0	9	1	3	2	0	0	1969	Frosted Orange
0	2	2	—	—	—	29	—	0	5	2	—	—	—	—	1968	*Mamestra brassicae*
0	0	4	2	4	1	8	0	1	1	0	6	0	1	0	1969	Cabbage Moth
6	13	17	—	—	—	46	—	7	41	26	—	—	—	—	1968	*Noctua pronuba*
9	0	14	21	6	7	16	22	5	6	5	15	10	4	7	1969	Large Yellow Underwing
0	5	4	—	—	—	4	—	1	13	31	—	—	—	—	1968	*Diataraxia oleracea*
0	0	4	2	50	65	6	4	8	14	28	61	2	67	0	1969	Bright-line Brown-eye
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Euxoa nigricans*
0	0	0	0	0	1	0	0	0	4	0	0	0	0	0	1969	Garden Dart
0	27	31	—	—	—	44	—	2	191	162	—	—	—	—	1968	*Apamea secalis*
0	0	42	8	69	33	14	57	2	15	181	56	113	30	10	1969	Common Rustic
0	0	1	—	—	—	0	—	3	11	8	—	—	—	—	1968	*Melanchra persicariae*
0	0	3	1	8	8	0	6	9	15	15	13	1	10	13	1969	Dot Moth
68	0	2	—	—	—	0	—	78	2	4	—	—	—	—	1968	*Operophtera brumata*
18	0	14	1	1	0	0	0	49	0	5	1	2	0	0	1969	Winter Moth

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TABLE

The Rothamsted Insect Survey—Light Traps: two years'

Pest Species	Year	109 Holme Fen	126 Aberystwyth	94 Monks Wood	23 St. Ives	88 Brooms Barn	125 Sandy	18 Flatford Mill	123 Carmarthen	106 Haverfordwest	1 Rothamsted (Barnfield)	34 Rothamsted (Allotments)	22 Rothamsted (Geescroft)	87 Writtle	17 Dale Fort	121 Port Talbot	90 Isleworth
Gortyna micacea Rosy Rustic	1968	—	—	—	1	2	—	23	—	—	2	0	1	4	6	—	0
	1969	7	18	171	0	4	5	27	0	11	9	5	5	11	5	1	0
Bupalus piniaria Bordered White	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
	1969	0	1	0	0	5	8	0	0	0	0	0	0	0	0	0	0
Panolis flammea Pine Beauty	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
	1969	0	1	0	0	0	8	0	0	0	0	0	0	0	0	0	0
Cerapteryx graminis Antler Moth	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
	1969	1	4	0	0	0	29	4	1	0	1	0	0	0	0	1	0
Erannis aurantiaria Scarce Umber	1968	—	—	—	0	0	—	2	—	—	0	0	28	0	0	—	0
	1969	0	1	0	0	1	2	1	0	0	0	0	24	0	0	0	0
Operophtera fagata Northern Winter Moth	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
	1969	3	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
Apamea sordens Rustic Shoulder-knot	1968	—	—	—	2	5	—	0	—	—	4	1	0	7	0	—	0
	1969	1	0	0	0	0	2	2	0	0	1	0	0	0	0	1	0
Gortyna flavago Frosted Orange	1968	—	—	—	0	0	—	4	—	—	2	0	3	3	1	—	3
	1969	14	0	8	2	4	3	3	3	2	3	2	2	4	8	0	0
Mamestra brassicae Cabbage Moth	1968	—	—	—	9	1	—	9	—	—	1	0	1	3	1	—	6
	1969	9	0	1	8	10	1	0	0	2	2	0	3	7	0	3	0
Noctua pronuba Large Yellow Underwing	1968	—	—	—	2	6	—	4	—	—	7	9	72	31	6	—	4
	1969	7	16	3	4	3	2	0	7	6	1	1	86	6	18	1	0
Diataraxia oleracea Bright-line Brown-eye	1968	—	—	—	4	6	—	10	—	—	4	4	2	31	39	—	1
	1969	29	13	1	4	7	11	7	0	5	3	5	2	20	31	16	1
Euxoa nigricans Garden Dart	1968	—	—	—	0	0	—	0	—	—	0	0	0	6	0	—	0
	1969	0	0	0	0	0	0	0	45	0	0	0	0	0	0	11	0
Apamea secalis Common Rustic	1968	—	—	—	18	20	—	65	—	—	21	9	29	43	28	—	4
	1969	16	44	11	4	8	6	22	20	204	17	9	23	0	24	10	2
Melanchra persicariae Dot Moth	1968	—	—	—	1	11	—	3	—	—	3	0	0	6	9	—	0
	1969	0	44	5	2	23	4	5	1	5	6	0	2	3	15	4	0
Operophtera brumata Winter Moth	1968	—	—	—	0	1	—	11	—	—	2	1	107	0	3	—	10
	1969	20	4	1	0	0	2	12	0	6	2	1	153	1	5	1	2

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130 Bath	16 Mortimer	69 Wisley	46 Alice Holt Lodge	62 Wye	92 Nettlecombe Court	104 Wellington	33 Dungeness	74 Cullompton	78 Ringwood	107 Axminster	67 Slapton Ley	113 Liskeard	114 Rosewarne	102 Helston (Church Hill)	Year	Pest Species
—	4	8	0	7	7	—	20	2	8	—	9	—	—	72	1968	*Gortyna micacea*
1	3	27	11	13	21	0	26	2	2	6	23	31	17	67	1969	Rosy Rustic
—	0	0	0	0	0	—	0	0	0	—	0	—	—	0	1968	*Bupalus piniaria*
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1969	Bordered White
—	1	0	0	0	0	—	0	0	0	—	0	—	—	0	1968	*Panolis flammea*
0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1969	Pine Beauty
—	0	0	3	0	0	—	3	0	0	—	0	—	—	1	1968	*Cerapteryx graminis*
0	0	0	7	0	0	0	20	0	1	0	0	0	0	1	1969	Antler Moth
—	7	3	10	0	2	—	0	0	12	—	0	—	—	0	1968	*Erannis aurantiaria*
0	0	1	0	0	2	0	0	0	0	0	0	0	0	1	1969	Scarce Umber
—	0	3	22	0	0	—	0	0	0	—	0	—	—	0	1968	*Operophtera fagata*
0	0	7	0	4	0	0	0	0	5	0	0	0	0	0	1969	Northern Winter Moth
—	0	1	0	3	0	—	2	0	0	—	0	—	—	0	1968	*Apamea sordens*
1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1969	Rustic Shoulder-knot
—	0	2	2	7	4	—	5	0	0	—	1	—	—	0	1968	*Gortyna flavago*
0	3	4	0	4	4	0	2	0	3	12	2	13	0	0	1969	Frosted Orange
—	1	0	0	1	0	—	7	12	0	—	6	—	—	30	1968	*Mamestra brassicae*
4	0	5	0	3	0	0	2	14	0	4	7	2	4	0	1969	Cabbage Moth
—	43	20	18	14	8	—	6	9	2	—	1	—	—	10	1968	*Noctua pronuba*
6	3	15	9	0	13	5	4	10	3	10	3	12	7	10	1969	Large Yellow Underwing
—	2	6	0	9	7	—	11	12	0	—	5	—	—	0	1968	*Diataraxia oleaea*
12	2	3	0	0	7	3	12	17	2	2	14	0	14	0	1969	Bright-line Brown-eye
—	0	0	0	0	0	—	0	0	0	—	0	—	—	0	1968	*Euxoa nigricans*
4	0	0	0	1	0	0	2	0	0	0	0	0	2	0	1969	Garden Dart
—	46	64	12	7	29	—	49	15	6	—	12	—	—	0	1968	*Apamea secalis*
45	2	49	13	2	87	6	28	23	17	55	31	20	14	5	1969	Common Rustic
—	2	2	0	14	0	—	0	1	0	—	12	—	—	0	1968	*Melanchra persicariae*
13	1	0	2	1	6	2	0	5	0	2	93	28	7	0	1969	Dot Moth
—	34	25	12	0	44	—	0	11	8	—	9	—	—	1	1968	*Operophtera brumata*
3	60	17	2	10	20	0	0	6	2	25	4	0	1	2	1969	Winter Moth

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TABLE

The Rothamsted Insect Survey—Light Traps: two years'

Pest Species	Year	59 Morangie	57 Ardross	58 Newton, Elgin	50 Grula, Skye	49 Fort Augustus	83 Killiecrankie (Pass)	29 Rannoch	60 Aros	48 Kindrogan	47 Dundee	82 Dunblane	97 Rowardennan	98 Auchencruive	39 Chester le Street	108 Egremont	72 Castletown, I.O.M.
Abraxas grossulariata	1968	—	0	0	—	0	—	0	1	—	0	0	0	0	18	—	11
Magpie Moth	1969	0	0	0	30	0	0	0	0	0	0	0	0	2	7	0	6
Agrotis segetum	1968	—	0	1	—	0	—	0	0	—	0	0	0	0	0	—	1
Turnip Moth	1969	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3
Erannis defoliaria	1968	—	9	8	—	47	—	9	0	—	1	0	75	0	0	—	14
Mottled Umber	1969	0	1	3	2	5	9	0	0	0	0	0	24	0	0	0	8
Phlogophora meticulosa	1968	—	0	0	—	0	—	1	1	—	0	0	0	0	0	—	21
Angle Shades	1969	0	0	0	5	1	1	0	0	0	0	0	0	0	0	0	3
Alsophila aescularia	1968	—	4	10	—	2	—	0	1	—	1	1	198	0	0	—	0
March Moth	1969	0	12	4	2	4	1	0	1	0	0	1	19	0	0	0	0
Hepialus humuli	1968	—	1	0	—	0	—	1	0	—	0	3	0	1	1	—	0
Ghost Swift	1969	0	0	1	3	0	0	3	0	0	0	3	0	4	0	4	0
Hepialus lupulina	1968	—	0	0	—	0	—	0	0	—	2	0	2	0	1	—	0
Common Swift	1969	0	0	0	0	0	0	15	0	0	0	0	3	2	0	1	3
Agrotis ipsilon	1968	—	1	1	—	0	—	0	0	—	0	0	0	0	0	—	9
Dark Sword Grass	1969	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	4
Euproctis chrysorrhoea	1968	—	0	0	—	0	—	0	0	—	0	0	0	0	0	—	0
Brown-tail	1969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrotis exclamationis	1968	—	0	3	—	0	—	0	0	—	6	4	0	3	5	—	59
Heart and Dart	1969	0	0	24	0	0	1	0	0	0	1	5	0	16	4	14	115
Plusia gamma	1968	—	1	3	—	3	—	1	4	—	0	1	0	1	47	—	60
Silver Y	1969	0	6	6	2	49	3	0	3	3	1	14	3	3	122	27	66
Laphygma exigua	1968	—	0	0	—	0	—	0	0	—	0	0	0	0	0	—	0
Small Mottled Willow	1969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nycterosea obstipata	1968	—	0	0	—	0	—	0	0	—	0	0	0	0	0	—	0
The Gem	1969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nomophila noctuella	1968	—	0	0	—	0	—	—	0	—	1	—	0	0	0	—	—
Rush Veneer Pearl	1969	0	0	0	0	0	—	—	0	—	0	—	—	1	0	—	—
Plutella maculipennis	1968	—	44	0	—	12	—	—	56	—	70	—	1	80	9	—	—
Diamond back Moth	1969	0	0	0	1	49	—	—	0	—	844	—	—	30	0	—	—
Udea ferrugalis	1968	—	0	0	—	0	—	—	3	—	0	—	0	0	0	—	—
Rusty Dot Pearl	1969	0	0	0	0	0	—	—	0	—	0	—	—	0	0	—	—

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2(c)

records of the moths of economic interest (1968 and 1969)

45 Malham Tarn	40 Lancaster	68 Harrogate	101 Keighley	96 Riseholme	95 Gibraltar Point	35 Bangor	71 Rhyd y Creuau	77 Maentwrog	79 Shardlow	61 Sutton Bonington	117 Burton upon Trent	53 Preston Montford	119 Darlaston	112 Shirley	Year	Pest Species
0	1	28	—	—	—	0	—	3	9	7	—	—	—	—	1968	*Abraxas grossulariata*
0	0	9	4	8	1	1	24	4	5	6	11	8	0	29	1969	Magpie Moth
0	0	1	—	—	—	1	—	0	0	5	—	—	—	—	1968	*Agrotis segetum*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1969	Turnip Moth
18	0	5	—	—	—	0	—	1844	3	0	—	—	—	—	1968	*Erannis defoliaria*
6	0	5	1	1	0	0	0	2422	2	0	0	0	0	0	1969	Mottled Umber
0	1	2	—	—	—	13	—	8	6	0	—	—	—	—	1968	*Phlogophora meticulosa*
0	4	0	0	14	5	3	0	1	10	4	2	9	1	0	1969	Angle Shades
0	0	5	—	—	—	0	—	65	5	6	—	—	—	—	1968	*Alsophila aescularia*
0	0	10	0	0	0	3	10	43	3	2	0	5	0	1	1969	March Moth
0	3	0	—	—	—	0	—	0	2	1	—	—	—	—	1968	*Hepialus humuli*
0	0	0	2	1	0	0	1	0	1	5	0	0	0	0	1969	Ghost Swift
0	1	9	—	—	—	0	—	0	77	24	—	—	—	—	1968	*Hepialus lupulina*
0	2	9	0	1	0	1	0	0	28	12	0	0	0	0	1969	Common Swift
0	0	1	—	—	—	4	—	8	0	0	—	—	—	—	1968	*Agrotis ipsilon*
0	0	0	0	0	1	0	0	1	2	0	1	0	0	0	1969	Dark Sword Grass
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Euproctis chrysorrhoea*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1969	Brown-tail
0	15	20	—	—	—	25	—	2	314	121	—	—	—	—	1968	*Agrotis exclamationis*
0	0	11	3	66	17	45	29	2	60	23	129	40	35	37	1969	Heart and Dart
12	5	13	—	—	—	17	—	13	15	14	—	—	—	—	1968	*Plusia gamma*
34	10	45	43	76	120	18	19	7	36	46	24	36	3	114	1969	Silver Y
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Laphygma exigua*
0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1969	Small Mottled Willow
0	0	0	—	—	—	0	—	0	0	0	—	—	—	—	1968	*Nycterosea obstipata*
0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	1969	The Gem
—	—	—	—	—	—	0	—	1	—	0	—	—	—	—	1968	*Nomophila noctuella*
0	—	—	—	13	8	0	2	0	—	8	0	7	—	—	1969	Rush Veneer Pearl
—	—	—	—	—	—	5	—	3	—	2	—	—	—	—	1968	*Plutella maculipennis*
0	—	—	—	73	0	4	3	1	—	9	2	2	—	—	1969	Diamond-back Moth
—	—	—	—	—	—	0	—	17	—	0	—	—	—	—	1968	*Udea ferrugalis*
0	—	—	—	9	0	0	49	70	—	5	0	21	—	—	1969	Rusty Dot Pearl

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TABLE

The Rothamsted Insect Survey—Light traps: two years'

Pest Species	Year	109 Holme Fen	126 Aberystwyth	94 Monks Wood	23 St. Ives	88 Brooms Barn	125 Sandy	18 Flatford Mill	123 Carmarthen	106 Haverfordwest	1 Rothamsted (Barnfield)	34 Rothamsted (Allotments)	22 Rothamsted (Geescroft)	87 Writtle	17 Dale Fort	121 Port Talbot	90 Isleworth
Abraxas grossulariata	1968	—	—	—	7	3	—	20	—	—	9	1	96	1	183	—	5
Magpie Moth	1969	9	11	8	2	3	1	17	88	70	11	3	104	7	48	5	3
Agrotis segetum	1968	—	—	—	6	14	—	0	—	—	6	5	3	61	0	—	0
Turnip Moth	1969	4	0	0	0	1	4	0	0	1	0	0	2	0	0	0	0
Erannis defoliaria	1968	—	—	—	0	1	—	2	—	—	0	0	48	0	0	—	0
Mottled Umber	1969	5	1	0	0	0	7	7	0	1	1	0	20	0	0	0	0
Phlogophora meticulosa	1968	—	—	—	3	3	—	27	—	—	0	2	5	2	12	—	1
Angle Shades	1969	30	5	17	9	13	7	49	15	2	2	1	9	3	6	0	1
Alsophila aescularia	1968	—	—	—	3	4	—	23	—	—	4	1	35	6	1	—	0
March Moth	1969	17	4	0	0	2	5	16	0	3	0	1	39	1	3	2	0
Hepialus humuli	1968	—	—	—	0	0	—	2	—	—	3	0	7	0	0	—	0
Ghost Swift	1969	3	2	5	0	0	0	3	5	15	1	0	6	0	0	0	0
Hepialus lupulina	1968	—	—	—	37	1	—	8	—	—	9	0	12	7	7	—	0
Common Swift	1969	0	0	0	3	0	1	14	0	0	5	4	4	10	8	0	1
Agrotis ipsilon	1968	—	—	—	0	1	—	2	—	—	0	0	0	0	9	—	0
Dark Sword Grass	1969	1	1	0	0	2	0	0	0	0	0	0	1	0	10	0	0
Euproctis chrysorrhoea	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
Brown-tail	1969	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Agrotis exclamationis	1968	—	—	—	93	83	—	33	—	—	66	33	24	599	27	—	6
Heart and Dart	1969	30	7	12	14	18	10	5	27	226	31	4	8	48	39	8	0
Plusia gamma	1968	—	—	—	12	16	—	21	—	—	4	4	31	73	48	—	0
Silver Y	1969	65	101	30	49	49	20	82	124	78	35	23	38	140	102	121	1
Laphygma exigua	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
Small Mottled Willow	1969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nycterosea obstipata	1968	—	—	—	0	0	—	0	—	—	0	0	0	0	0	—	0
The Gem	1969	4	3	1	1	2	6	2	0	0	4	0	1	0	0	0	2
Nomophila noctuella	1968	—	—	—	—	10	—	0	—	—	3	1	0	0	0	—	0
Rush Veneer Pearl	1969	11	20	17	—	8	29	15	—	—	18	0	3	—	—	0	0
Plutella maculipennis	1968	—	—	—	—	75	—	0	—	—	548	406	9	1	3	—	51
Diamond-back Moth	1969	16	13	8	—	272	115	4	20	—	729	382	9	—	—	0	39
Udea ferrugalis	1968	—	—	—	—	0	—	3	—	—	2	0	1	0	0	—	0
Rusty Dot Pearl	1969	23	637	0	—	5	20	5	—	—	7	6	9	—	—	274	3

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2(d)

records of the moths of economic interest (1968 and 1969)

130 Bath	16 Mortimer	69 Wisley	46 Alice Holt Lodge	62 Wye	92 Nettlecombe Court	104 Wellington	33 Dungeness	74 Cullompton	78 Ringwood	107 Axminster	67 Slapton Ley	113 Liskeard	114 Rosewarne	102 Helston (Church Hill)	Year	Pest Species
—	215	1	0	7	18	—	4	56	3	—	10	—	—	223	1968	*Abraxas grossulariata*
0	81	2	1	0	11	9	12	34	0	0	7	19	1	108	1969	Magpie Moth
—	0	0	0	1	5	—	2	4	0	—	0	—	—	4	1968	*Agrotis segetum*
1	0	0	2	0	0	0	4	0	0	0	1	2	4	0	1969	Turnip Moth
—	24	21	19	0	15	—	0	1	11	—	2	—	—	2	1968	*Erannis defoliaria*
0	7	10	9	4	15	0	0	0	3	11	1	0	1	1	1969	Mottled Umber
—	4	2	0	3	25	—	1	3	1	—	4	—	—	5	1968	*Phlogophora meticulosa*
1	2	1	0	5	10	0	1	7	2	9	1	13	1	12	1969	Angle Shades
—	6	7	10	3	6	—	0	6	5	—	15	—	—	0	1968	*Alsophila aescularia*
3	7	7	17	7	17	0	0	1	6	125	10	0	3	1	1969	March Moth
—	1	2	5	1	0	—	0	1	0	—	1	—	—	2	1968	*Hepialus humuli*
0	0	1	3	1	0	0	0	0	1	1	1	1	5	2	1969	Ghost Swift
—	19	2	2	23	0	—	55	2	2	—	1	—	—	0	1968	*Hepialus lupulina*
2	4	0	0	1	0	0	15	0	0	0	0	0	1	0	1969	Common Swift
—	0	1	0	0	12	—	1	1	1	—	1	—	—	8	1968	*Agrotis ipsilon*
0	0	3	0	0	1	0	2	1	0	1	2	1	2	0	1969	Dark Sword Grass
—	0	0	0	0	0	—	83	0	0	—	0	—	—	0	1968	*Euproctis chrysorrhoea*
0	0	0	0	0	0	0	426	0	0	0	0	0	0	0	1969	Brown-tail
—	30	66	48	361	56	—	139	25	0	—	44	—	—	68	1968	*Agrotis exclamationis*
6	19	48	18	2	34	15	47	19	9	43	41	209	61	68	1969	Heart and Dart
—	26	112	37	45	119	—	22	120	2	—	35	—	—	30	1968	*Plusia gamma*
21	36	171	17	22	179	1	45	128	5	302	120	102	101	63	1969	Silver Y
—	0	0	0	0	0	—	0	0	0	—	1	—	—	0	1968	*Laphygma exigua*
3	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1969	Small Mottled Willow
—	0	0	0	0	0	—	0	0	0	—	1	—	—	0	1968	*Nycterosea obstipata*
0	1	2	0	0	2	0	2	12	2	0	13	0	10	0	1969	The Gem
—	—	0	0	1	2	—	—	12	—	—	38	—	—	—	1968	*Nomophila noctuella*
—	—	0	0	0	32	—	—	79	—	—	65	—	71	—	1969	Rush Veneer Pearl
—	—	0	0	0	4	—	—	125	—	—	77	—	—	—	1968	*Plutella maculipennis*
—	—	34	28	0	7	—	—	60	—	—	36	—	304	—	1969	Diamond-back Moth
—	—	0	0	0	80	—	—	99	—	—	90	—	—	—	1968	*Udea ferrugalis*
—	—	15	0	1	127	—	—	330	—	—	341	—	623	—	1969	Rusty Dot Pearl

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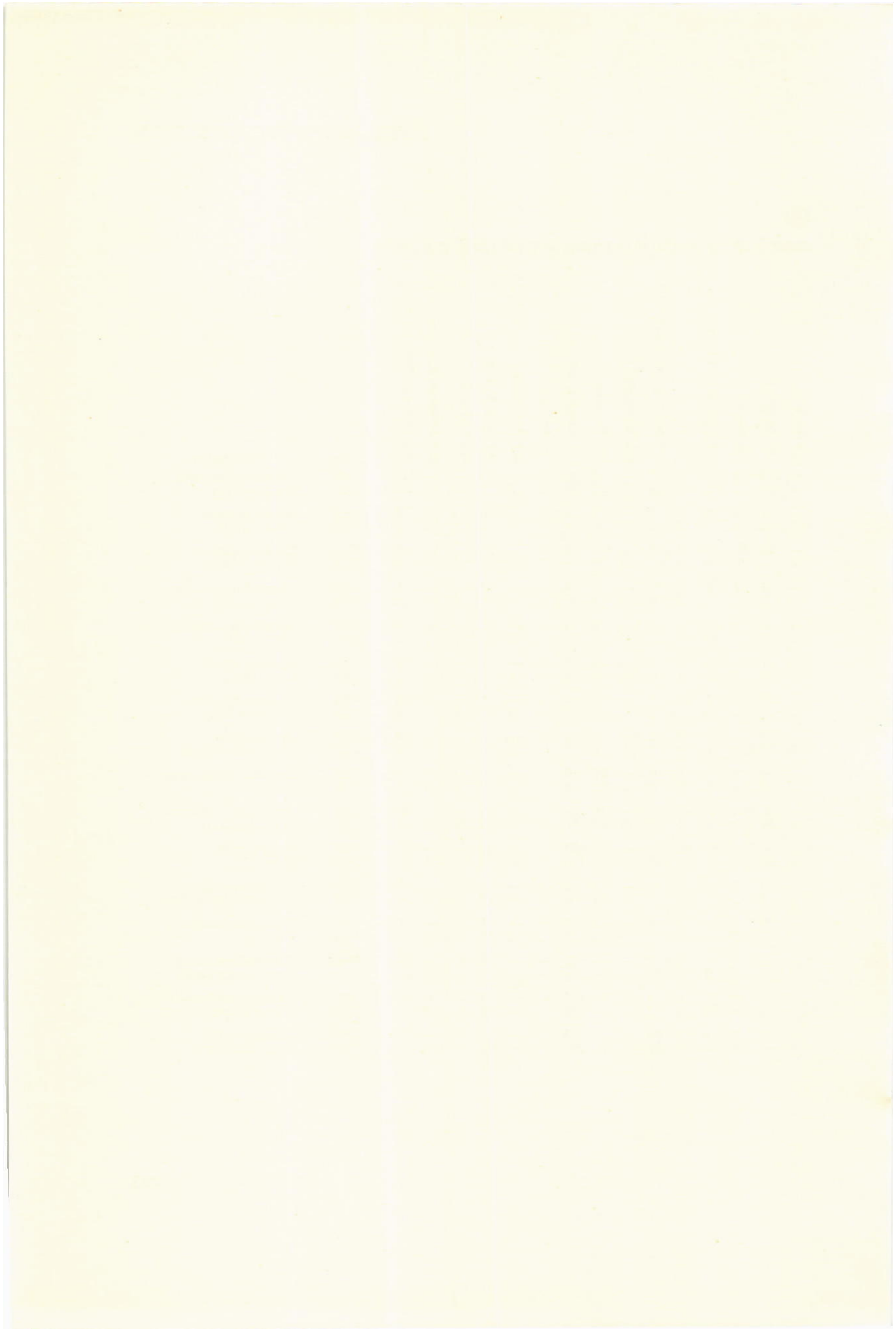

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CONVERSION FACTORS

Factors for the Conversion of Imperial to Metric Units

1 inch (in.)	= 2·540 centimetres (cm)
1 foot (ft) (=12 in.)	= 30·48 cm
1 yard (yd) (=3 ft)	= 0·9144 metre (m)
1 square yard (sq yd)	= 0·8361 sq m
1 acre (=4840 sq yd)	= 0·4047 hectare (ha)
1 ounce (oz)	= 28·35 grams (g)
1 pound (lb)	= 0·4536 kilogram (kg)
1 hundredweight (cwt) (=112 lb)	= 50·80 kg
1 ton (=2240 lb)	= 1016 kg = 1·016 metric tons (tonnes) (t)
1 pint	= 0·5682 litre
1 gallon (gal) (=8 pints)	= 4·546 litres
1 fluid ounce = 1/20 pint	= 0·02841 litre = 28·41 ml
1 cubic foot	= 28·32 litres

To convert	*Multiply by*
oz/acre to g/ha	70·06
lb/acre to kg/ha	1·121
cwt/acre to kg/ha	125·5
cwt/acre to tonnes/ha	0·1255
tons/acre to kg/ha	2511
tons/acre to tonnes/ha	2·511
gal/acre to litre/ha	11·233

The following factors are accurate to about 2 parts in 100:

1 lb/acre = 1·1 kg/ha
1 gal/acre = 11 litre/ha
1 ton/acre = 2·5 tonnes/ha

In general reading of the text there will be no great inaccuracy in regarding:

1 lb = 0·5 kg
1 lb/acre = 1 kg/ha

Temperatures

To convert °F into °C subtract 32 and multiply by $\frac{5}{9}$ (0·556)
To convert °C into °F multiply by $\frac{9}{5}$ (1·8) and add 32

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Factors for the Conversion of Metric to Imperial Units

1 centimetre (cm)	=	0·3937 inch (in.) = 0·03281 ft
1 metre (m)	=	1·094 yards (yd)
1 square metre (sq m)	=	1·196 square yards (sq yd)
1 hectare (ha)	=	2·471 acres
1 gram (g)	=	0·03527 ounce (oz)
1 kilogram (kg)	=	2·205 pounds (lb)
1 kg	=	0·01968 hundredweight (cwt) = 0·0009842 ton
1 metric ton (tonne) (t)	=	0·9842 ton
1 litre	=	1·760 pints = 0·2200 gallon (gal)

1 litre = 1000 millilitres (ml) = 35·20 fluid ounces = 0·03531 cubic foot

To convert	*Multiply by*
g/ha to oz/acre	0·01427
kg/ha to lb/acre	0·8921
kg/ha to cwt/acre	0·007966
tonnes/ha to cwt/acre	7·966
kg/ha to tons/acre	0·0003983
tonnes/ha to tons/acre	0·3983
litre/ha to gal/acre	0·08902

Plant nutrients

Plant nutrients are best stated in terms of amounts of the elements (P, K, Na, Ca, Mg, S); the old 'oxide' terminology P_2O_5, K_2O, Na_2O, CaO, MgO, SO_3) is still used in work involving fertilisers and liming since Regulations require statements of P_2O_5, K_2O, etc.

For quick conversions

(accurate to within 2%) the following factors may be used:

$2\frac{1}{3} \times P = P_2O_5$	$\frac{3}{7} \times P_2O_5 = P$
$1\frac{1}{5} \times K = K_2O$	$\frac{5}{6} \times K_2O = K$
$1\frac{2}{5} \times Ca = CaO$	$\frac{7}{10} \times CaO = Ca$
$1\frac{2}{3} \times Mg = MgO$	$\frac{3}{5} \times MgO = Mg$

For accurate conversions:

To convert	*Multiply by*	*To convert*	*Multiply by*
P_2O_5 to P	0·4364	P to P_2O_5	2·2915
K_2O to K	0·8301	K to K_2O	1·2047
CaO to Ca	0·7146	Ca to CaO	1·3994
MgO to Mg	0·6031	Mg to MgO	1·6581

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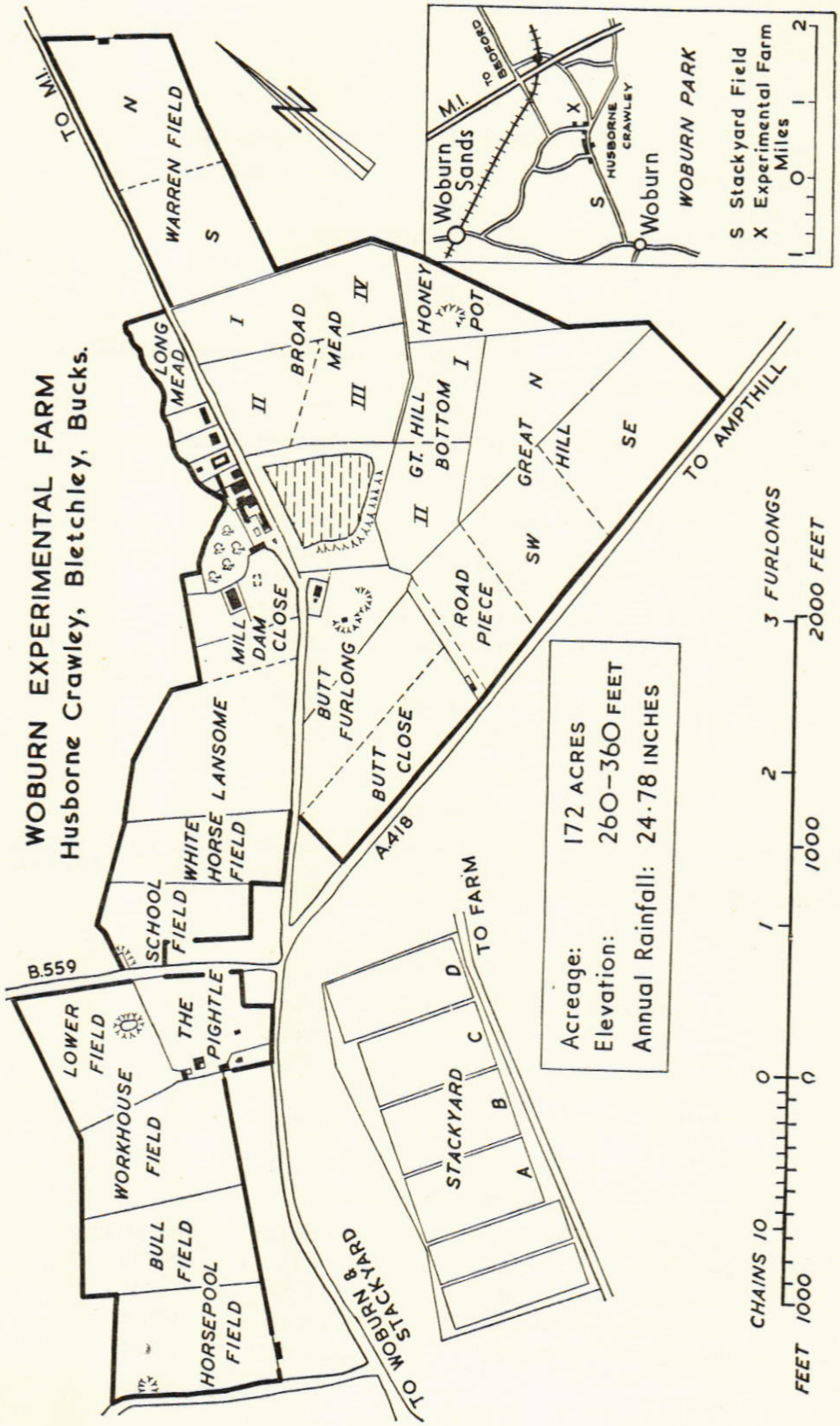

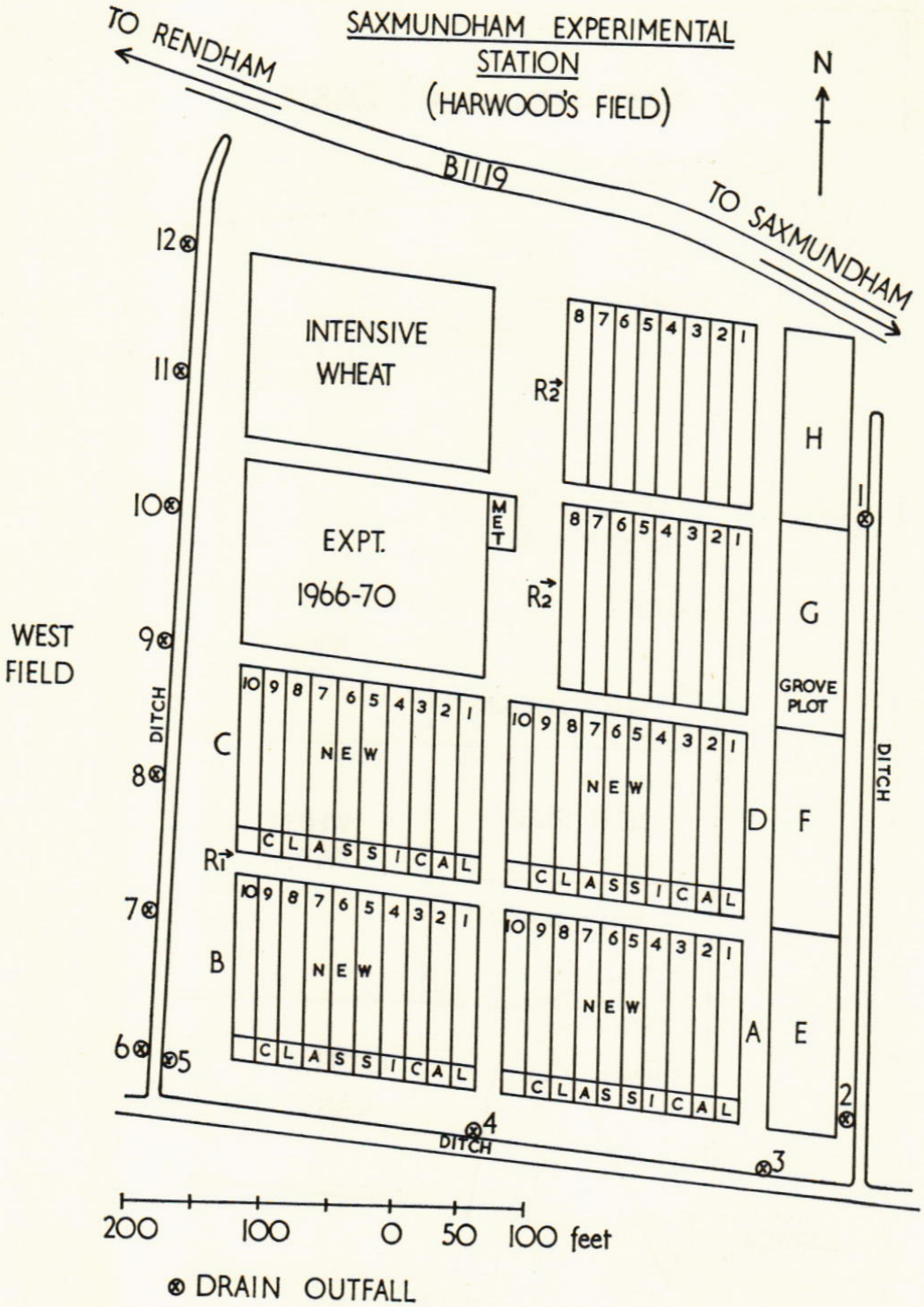

Treatment numbers on Rotation I (R1) and Rotation II (R2) are shown on individual plots—1, 2, 3, etc.
The blocks of Rotation I are shown as A, B, C, D.
Sections of Grove Plot are shown as E, F, G, H.

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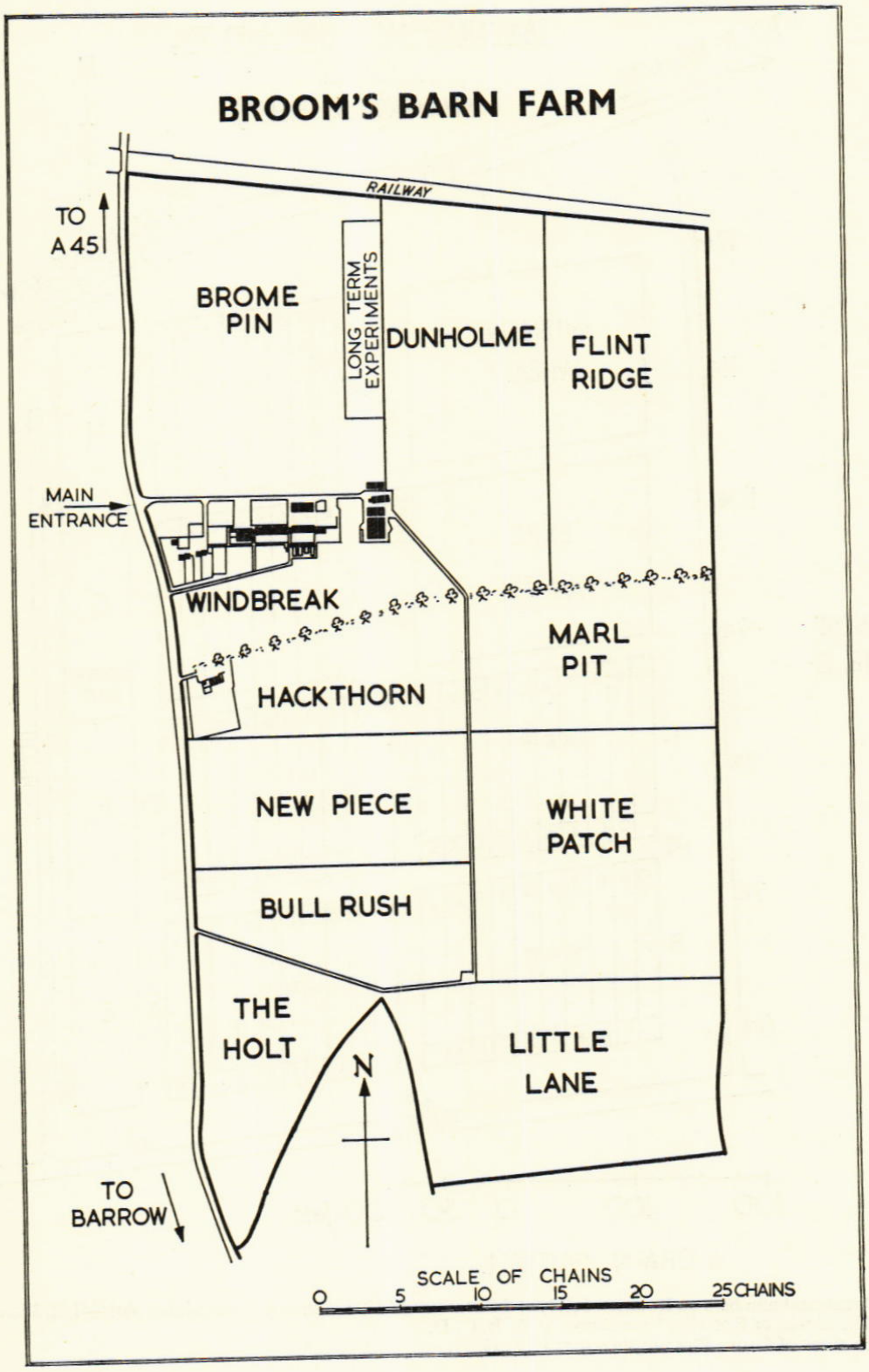

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