CROP RESIDUES AS CAUSATIVE AGENTS OF ROOT ROTS OF VEGETABLES

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There is a growing realization among plant pathologists and growers that the importance of root rot diseases has been underestimated in the past. Losses from such diseases are not always obvious and are difficult to measure, but for some crops these losses are, in the aggregate, greater than those caused by more dramatic and visible diseases of above-ground parts. In dealing with root rots there has been a tendency either to oversimplify the problem or to make it more complex than it really is. Oversimplification is expressed most often by attributing the whole disease complex to a single pathogenic organism of the familiar "classical" type. In the other direction, the complex is often ascribed to the operation of ill-defined agronomic factors which are not susceptible of experimental study.

Whatever its cause, root rot is a disease, an active, dynamic response by a plant to abnormal environmental conditions. A nematode, insect or microbial pathogen may or may not be a feature of this abnormal environment. Chemical and physical factors may play either a dominant or a subsidiary role in bringing about or maintaining the abnormal conditions. The undoubted success of the germ theory of disease causation should not blind us to the possibility that in the etiology of some diseases, microorganisms may be only incidental, secondary invaders following an initial injury caused by chemical or physical agents. In the strawberry root rot complex, for example, so many different organisms have been described as pathogenic (45) that it is permissible to doubt that this approach is valid. In this and other cases, workers have been impelled to investigate non-biological factors as well.

The factor which has received most consideration, and with which the present paper is concerned, is the soil organic matter. There are root rots, e.g., the Phymatotrichum root rot of cotton (25) and take-all of wheat (16), which are decreased in severity by certain types of organic matter. With this type of action we are not at present concerned. Usually such decreases by organic matter occur in root rots which are caused by a single pathogen of the classical type; an exception to this rule is the effect of soybean residues in causing a reduction of strawberry root rot (18).

In a consideration of the possible ways in which plant residues may increase root rot, there are at least four types of mechanism which may be responsible. In the simplest of these, a pathogenic organism may be stimulated in its growth or activity by the organic matter. A second pos-

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sible mechanism is the effect of added residues on the available nitrogen or phosphorus of the soil; Stumbo *et al* (41) found straw to increase take-all of wheat by this sort of action. Another possibility is the induction by organic matter of an unfavorable microbiological balance in the soil or the rhizosphere that leads eventually to plant injury (51). Finally, there may be in the added plant material chemical substances that cause root injury, or such substances may appear during the microbial decomposition of the residue. It is this last mechanism that the present work is designed to explore.

Previous work on this problem (6) was confined to laboratory experiments. It was found that seedling radish roots are killed within eight hours in water extracts of certain plant materials — ladino clover and timothy. Other plant residues under the same conditions caused no change (soybean) or caused it only under special circumstances (corn). In general, decomposition of the residue was accompanied by a progressive loss in toxicity. These results suggested that the same residues applied to soil in which plants are growing might cause a similar killing of root cells which would appear as a more or less typical root rot. Killing of even a small area of root tissue of a plant growing in soil would expose the root to invasion by saprophytes and low-grade parasites which are unable to attack the undamaged root.

In the work with radish seedlings several possible mechanisms were excluded by the nature of the experiments. Roots were soaked for eight hours in dilute water extracts of the plant material under test. In these circumstances it is very improbable that the injury is caused by a nutrient deficiency, an injurious microbiological flora, or a particular microbial pathogen. Injury of this type appears to result from the presence in the extract of chemicals which are toxic to root cells.

With this background, it was possible to plan greenhouse and field experiments to test the effect of plant residues in soil. In the greenhouse experiments to be reported, dried residues were added to soil directly. In the field a more natural plan was followed: crops were grown one year and the residues plowed under, as in normal farming operations. The data from these experiments are presented in this paper, as supporting the hypothesis of chemical injury as a primary factor in root rot.

Choice of plant residues to be tested in the field was based in part on the laboratory work, in part on results obtained at Storrs by the Department of Horticulture of the University of Connecticut. In this work (Experiment No. 1, Maintenance of organic matter and productivity of vegetable soils) some very striking effects of previous crops have been observed [1]. In particular, it has been found that a crop of sweet corn with a late-fall seeding of vetch after the corn stalks have been removed has an extremely severe effect on a succeeding crop of head lettuce or onion. Lettuce transplants set in such soil make almost no growth for

1. The author is indebted to Professor H. A. Rollins for permission to cite these results in advance of publication.

the first six to eight weeks, and grow only very poorly thereafter, never forming heads. The root systems are particularly affected; it is not uncommon to find that, as long as a month after transplanting, the roots have not grown out from the mass of soil that was carried with them from the coldframe where the plants were started. Onions suffer equally severely from a previous crop of corn and vetch: the stand is poor, growth is slow, and there is a high incidence of root rot, usually ascribed to the pathogenic fungus *Phoma terrestris*. A photograph of adjacent plots (Fig. 1) illustrates this effect on onions.

OBJECTIVES

The purpose of the experimental work to be described was to test under greenhouse and field conditions an hypothesis derived from laboratory studies, referred to above. Some of the possible factors that might obscure or complicate the data could be predicted from the literature. In particular, it was necessary to include soil treatments of three kinds: high nitrogen, high phosphorus, and the fumigant chloropicrin.

Nitrogen Treatment

The well-known nitrogen depletion effect of organic residues, mentioned earlier, represents a pitfall in the interpretation of crop residue data of all sorts. The idea that carbon compounds added to soil make possible extensive growth of soil microorganisms with a consequent locking-up of nitrogen in the form of unavailable protein, or loss of nitrogen through denitrification, was first advanced in 1899; the early history of the subject is reviewed by Collison and Conn (9). Allison (1) and Newton and Kiriloff (31) showed that the depressant action of straw on crop growth is the result of nitrogen depletion. Myers and Anderson (29) explain "bromegrass toxicity", first attributed by Benedict (3) to a directly injurious factor in bromegrass residues, on the basis of nitrogen loss. The data of Myers and Anderson do not, however, appear to support their conclusion; addition of ammonium sulfate at 200 lb. per acre did not fully counteract the effect of a previous crop of bromegrass. Myers and Hallsted (30) credit nitrogen depletion with a role in the deleterious effect of sorghum on a succeeding wheat crop (38). Thomas (42) found an inverse correlation in the field between nitrate nitrogen and severity of brown root rot of tobacco, and suggested tentatively that the loss of nitrates after, e.g., timothy sod is turned under, may lead to attack by soil fungi on tobacco roots as a source of nitrogen. Eisenmenger (14) found that brown root rot is most severe after crops whose residues have a high carbon/nitrogen ratio, i.e., decompose slowly and possibly cause nitrate depletion.

The possible interference of nitrogen starvation with the studies on root rot was eliminated in the greenhouse by liberal application of ammonium sulfate to the soil containing residues. Richards and Shrikhande (33) found the nitrogen-depleting effect of wheat straw to be counteracted by the simultaneous application of 0.8 gm. nitrogen per 100 gm.

Figure 1

The effect of previous crops on growth of onion at the University of Connecticut, Storrs, Conn. *Right:* previous crop corn followed by vetch. *Left:* previous crop spinach, followed by beets.

straw, and other workers (49) arrived at essentially the same figure. In the present work the level arbitrarily chosen in greenhouse studies was 1.0 gm. nitrogen per 100 gm. residue. Corn stover has about the same nitrogen content as cereal straw (37).

In the field the nitrogen factor was eliminated by application of commercial fertilizer to the whole field; by use of some injurious residues, which themselves supply nitrogen (e.g., clover), and by inclusion of a high nitrogen treatment in every series. It is in the last-named device that most confidence can be placed for, as will be shown, in no single series or harvest within a series was root injury decreased or yield increased by the application of Uramon at 200 lb. per acre. Uramon at much higher levels (4840-7260 lb. per acre) has been reported (7) to reduce black root rot of tobacco, but its role at such a level is more than that of a mere nitrogen supplement — perhaps at this dosage its primary effect is to increase the soil pH.

Phosphorus Treatment

Inclusion of superphosphate among the soil treatments was perhaps less justified than the test of nitrogen, since there is little evidence in the root rot literature concerning phosphate effects. Hoffer and Carr (19) found corn root rot to be increased by a deficiency of calcium and phosphate, and Stumbo *et al* (41) reported that take-all of wheat in soil receiving straw supplements was reduced to a minimum by addition of nitrogen and phosphate fertilizers. On the other hand, it has been claimed (36) that root rot of wheat is increased by application of superphosphate.

Chloropicrin Treatment

The purpose of including a chloropicrin treatment in the field experiment was twofold. In the first place, there have been reports (40) of yield increases after chloropicrin treatment which were not the result of pest control. This raised the possibility that, if plant residues were toxic, the chemical might in some way remove or neutralize or encourage the destruction of the injurious factor.

The second basis for inclusion of the chloropicrin treatment was to eliminate, if possible, the nematode factor, the chemical being a powerful nematocide. Since brown root rot of tobacco, one of the diseases most often cited as influenced or caused by plant residues, has been demonstrated to result from attack by the meadow nematode (2, 22, 23, 47), there was always the possibility of confusion in this work between nematode effects and previous crop effects.

GREENHOUSE EXPERIMENTS

Previous work (6) had shown the radish seedling to be sensitive to certain plant extracts. A few preliminary experiments were performed to test the response of radish seedlings in soil to additions of known amounts of dried and ground plant residues. The addition to soil of 2-5 per cent by weight of dried ryegrass or clover tops caused root browning of radish, in conformity with the earlier work on extracts.

It was found, however, that for work in soil, lettuce seedlings are more sensitive than radish, with the added advantage that grading can be more exact, since on the lettuce root the boundary between normal and discolored tissue is much more easily visible than on the radish root. A typical experiment with lettuce seedlings is displayed in Table 1, and demonstrates the effect of corn stover (with added nitrogen) on growth and root damage in lettuce.

The data of Table 1 are typical in that increasing the concentration of a toxic residue results in a progressive decline in plant weight and a rise in the extent of root rot. While the latter was not high when compared to field experience, the attainment in only 24 days of a level of about 14 per cent root damage is significant.[1]

Table 1 illustrates a second point: that the corn effect is not antidoted or eliminated by adding nitrogen in the form of ammonium sulfate. The rationale for nitrogen supplements has been discussed. Evidently, this nitrogen depletion is not a factor in these experiments, since the supplementary available nitrogen (1 gm. nitrogen per 100 gm. resi-

1. See below (p. 11) for the method of grading roots.

due) was in e cess of the amount reported in the literature (33, 49) to be adequate for the microbial decomposition of plant materials.

The addition of ammonium sulfate alone had no effect on root browning and affected fresh weight adversely only at a concentration four times as high as the highest used in the experiment under discussion.

In a similar experiment, the addition of clover at 2.5 per cent, supplemented with ammonium sulfate, reduced the dry weight of lettuce about 68 per cent and caused more than 12 per cent of root rot. The clover effect was not reduced by the addition of ammonium sulfate at nitrogen levels of 1 and 2 gm. per 100 gm. of residue.

TABLE 1

THE EFFECT OF ADDED CORN RESIDUES ON GROWTH AND ROOT BROWNING OF LETTUCE [1]

Per cent Residue[2]	Initial pH	Final pH	Per cent Mortality	Average Fresh Weight[3] gms.	Average Dry Weight[3] gms.	Root Grade[4]
0	6.89	6.43	0	10.4	0.79	0.8
1	6.80	6.58	0	5.6	0.49	1.3
2	6.50	6.01	41	3.3	0.28	2.1
5	6.68	6.51	44	2.2	0.18	3.2

1. Variety Big Boston; 18-day seedlings transplanted into soil-residue mixtures.
2. Dry basis. Ammonium sulfate added to supply 1 gm. nitrogen per 100 gm. residue.
3. Harvested at 24 days.
4. Average of all surviving plants. See text (p. 11) for method of grading roots.

Soil-residue mixtures used in the experiment summarized in Table 1 were incubated 30 days at high moisture (visibly wet) and high temperature (summer greenhouse temperatures). After 30 days the previous experiment was repeated under as nearly the same conditions as possible. The results of the experiment are shown in Table 2; for convenience, some of the data from Table 1 are included.

It is clear from Table 2 that incubation reduced the toxicity of these soil-residue mixtures below the level detectable with this assay. In fact, yields (fresh weight) were higher in the soil-residue mixtures than in the control. The increase in yield is not surprising: the control soil was supporting its second crop of lettuce without having been fertilized in any way, while the soil-residue mixtures benefited from the fertilizer effect of the added plant material and ammonium sulfate. Under conditions favoring microbial action the toxicity thus disappears, as in the earlier reported studies on the toxicity of extracts of "pure" residues to radish seedling roots. The causative role of microorganisms is of course not rigorously proved, since there were no sterile stability controls, but it is very likely.

How closely the total organic matter added in these experiments approximates that in field soils is not certain. The maximum added amounted to 5 per cent organic matter by weight, and adverse effects on growth were noted at as low as 1 per cent; by comparison soils in sod for some years may have as high as 9.6 per cent organic matter (50).

TABLE 2

THE EFFECT OF INCUBATION ON THE TOXICITY OF CORN RESIDUES TO LETTUCE [1]

	Before Incubation [5]			After Incubation [5]		
Per cent Residue [2]	Per cent Mortality	Average Fresh Weight [3] gms.	Root Grade [4]	Per cent Mortality	Average Fresh Weight [3] gms.	Root Grade [4]
0	0	10.4	0.8	8	5.3	0.4
1	0	5.6	1.3	3	5.9	0.3
2	41	3.3	2.1	0	6.2	0.4
5	44	2.2	3.2	5	8.5	0.2

1. Variety Big Boston; 18-day seedlings transplanted into soil-residue mixtures.
2. Dry basis. Ammonium sulfate added to supply 1 gm. nitrogen per 100 gm. residue.
3. Harvested at 24 days.
4. Average of all surviving plants. See text (p. 11) for method of grading roots.
5. Period of incubation 30 days.

These greenhouse experiments, and others not described in detail, serve to confirm the earlier laboratory work in two respects: certain plant residues cause injury, and the injurious factor disappears with time. In addition, they demonstrate that adding nitrogen did not prevent injury. The problem remaining was to demonstrate the same or similar effects under field conditions.

FIELD EXPERIMENTS

Experimental Design and Criteria of Results

The field experiments were carried out on a uniform, gently sloping plot 200 by 160 feet in size. This field had been in continuous cultivation prior to 1946, when the experiment was begun with the growing of the crops whose effect on succeeding crops was to be tested.

In 1946 the field was divided into four areas, one for each comparison planned: timothy as a previous crop compared to soybean (variety Manchu), medium red clover compared to soybean, and two series of sweet corn (variety Golden Cross Bantam), plus a late fall seeding of vetch, compared to bare fallow. In each area the space available was divided into eight equal portions, of which four were assigned at random to one of the cover crops, four to the other. The indicated crops were planted in April and May, the corn in three-foot rows, the other crops broadcast.

It should be noted that the stand of soybean in 1946 was very sparse and, by midsummer, the plots were heavily overgrown with weeds, almost entirely *Amaranthus retroflexus*. This fact must be borne in mind in evaluating data from soybean plots.

In September, 1946, the corn was cut and the stalks were removed from the field, leaving the stubble. These plots were disked thoroughly and vetch was broadcast on September 13. The clover, timothy and soybean were left standing as cover crops over winter. The vetch in the corn plots made some growth before frost, and the field was not worked further until spring.

The entire field was plowed in April, 1947, and fertilizer was applied (1000 lb. of 7-14-14 per acre) immediately. Within a given series (consisting of eight equal areas, four with one previous crop, four with another) each area was subdivided into four, and soil treatments as described below were randomized among them. The test crops were then planted across the whole area devoted to the comparison.

The design of each series was thus 2 x 4 x 4: two crop residues, four soil treatments, and four replicates.

The soil treatments were applied April 18-20, 1947, as follows:

1. Uramon (42 per cent nitrogen), 300 lb. per acre;
2. Chloropicrin, 545 lb. per acre, applied by machine in 10-inch rows[1];
3. Superphosphate, 400 lb. per acre;
4. No treatment (control).

Test crops were planted as follows:

Series I (corn and vetch *vs.* fallow in 1946):

A. Head lettuce, variety Big Boston, set in the field May 7;

B. Onion sets, variety Ebenezer, planted May 8;

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1. Acknowledgment is made of the generous assistance of Innis Speiden and Co., who provided and applied the chloropicrin.

Series II (timothy *vs.* soybean in 1946):

A. Head lettuce, variety Big Boston, set in the field May 7;

B. Spinach, variety Savoy-Leaved Long Standing, sown May 8;

C. Potato, variety Katahdin, cut seed planted May 8;

Series III (clover *vs.* soybean in 1946): leaf lettuce, variety Grand Rapids, sown July 1 in the field.

All 1947 crops were planted in three-foot rows to facilitate cultivation, while the distance between plants in the row varied with the requirements of the crop. Plots were planted solidly, but no plants were harvested that were within two feet of the boundary of the plot. The number and spacing of harvests varied with the test crop.

In harvesting, the plants were dug up, with an attempt to recover all of the roots. The roots of each plant were cut from the top at the soil line and the roots were graded individually. The tops from a given plot were weighed *en masse.* Data tabulated include the average root grade and, when taken, the average fresh weight per plant. The significance of means was tested by analysis of variance (39).

The well-known inaccuracy of fresh weight data makes it difficult to draw conclusions from small differences, but in most of the field experiments the differences between crop residues in their effect on a succeeding crop were so large that the fresh weight criterion was valid. Some soil treatment effects which, when present, were of smaller magnitude, may have been lost or obscured by the limitation of yield data to fresh weights.

Root damage is to be relied upon more than is fresh weight in assaying the effect of previous crops. In the case of lettuce, the typical symptom, illustrated in Figure 2, was the appearance on both main and feeder roots of areas of discoloration. The color ranged from reddish brown to brown and the discolored areas were discontinuous, i.e., a severely affected root had alternating bands of normal and discolored tissue. On spinach, the discoloration tended to be yellow-brown to brown in color and the affected areas were larger and more irregular in size than similar areas on lettuce roots. In the case of onion, the only symptom observed was the well-known pink root. Potato roots were usually only slightly affected: feeder roots showed brown areas of varying length at their tips.

The extent of the area discolored was judged by visual inspection of each plant harvested. The method proposed by Horsfall and Barratt (20) proved to be applicable to root rot data without substantial change. In this method, a scale is set up ranging from no discoloration to a hypothetical complete discoloration. The scale is based on 50 per cent

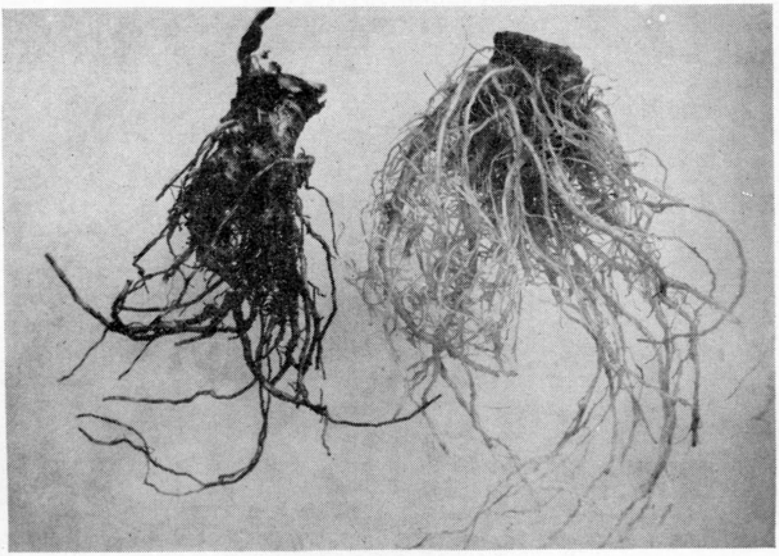

Figure 2

The effect of the previous crop on lettuce root injury (Series II). *Right:* previous crop soybean. *Left:* previous crop timothy. Photographs made at time of heading of lettuce.

discoloration as a midpoint, with grades differing by a factor of two in either direction, as follows:

Per cent Discoloration	*Grade*
0	0
0-3	1
3-6	2
6-12	3
12-25	4
25-50	5
50-75	6
75-88	7
88-94	8
94-97	9
97-100	10
100	11

All grading was done by a reliable technician who had no information on the layout of the field, i.e., did not know what treatment had been applied to a given plot. The number of individual plants examined per replicate plot at each harvest was never less than 10, and more usually was about 15. Conclusions as to soil treatment effects at any given harvest date are, therefore, based on 40-60 individual plants, while conclusions as to crop residue effects are based on 160-240 plants.

The mean grade for each replicate plot was used in all statistical calculations. Conversion of mean grade to per cent disease is facilitated by construction of a calibration curve, but the mean grade itself is a more useful statistic than a percentage figure derived from it.

Series I: The Effect of Corn and Vetch on Root Rot

A. Head Lettuce

In this series, comparison was made between head lettuce after fallow and the same test crop after a previous crop of sweet corn followed by a late-fall seeding of vetch. Considering first the data on root browning at the three harvest dates (Table 3), there is evident a highly significant effect of the previous crop. In all cases the amount of root rot was greater in the corn-vetch than in the fallow plots. In the first harvest, at 34 days, the average root length browned in all fallow plots was 3.0 per cent (grade 1.3), in all corn-vetch plots 8.0 per cent (grade 2.4). In the second harvest, at 53 days from transplanting, the corresponding figures were 4.0 and 38.5 per cent, and in the 73-day harvest 9.0 and 59.5 per cent.

These are the most clear-cut differences found in any of the experiments to be reported. The root damage was less in fallow plots than in the soybean "controls" of the two other lettuce experiments, suggesting the possibility that even soybean — or the associated weed — residues are somewhat injurious. Further to emphasize the difference in this series, the root damage after corn and vetch was as high as that after timothy and much higher than that after clover, at the corresponding harvest dates. In other words, Series I compares the two extreme treatments: corn and vetch the previous year, and fallow.

The deleterious effect of the preceding crop is as strikingly demonstrated by the yield data of Table 3 as it is by the data on root symptoms. In the first harvest the average plant fresh weight in the fallow plots was 67 per cent greater than in the corn-vetch plots; in the second harvest it was 59 per cent greater. Both differences are highly significant.

Soil treatments in this series had no consistent or significant effect on the extent of root damage, nor did they affect significantly the yields in the first harvest. In the second harvest there was a significant effect of soil treatments. Further analysis of these data showed that chloropicrin caused a significant increase in plant weight in the fallow plots, but had no such effect after corn. It appears that, as in other series, the chloropicrin effect on yield is not related to the crop residue factor. Possibly in the corn-vetch plots of this series the expected increase in yield from chloropicrin was not attained because of the over-riding and quantitatively more important effect of the previous crop.

TABLE 3

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON ROOT BROWNING AND YIELD OF HEAD LETTUCE [1]

		Root Grade [3]		Fresh Weight (grams per plant)	
Harvest, days	Soil Treatment [2]	After Corn and Vetch	After Fallow	After Corn and Vetch	After Fallow
34	Ur.	2.0	1.0	62.9	95.7
	Chlor.	2.1	1.5	71.0	100.1
	SP	2.8	1.1	51.9	111.1
	Check	2.6	1.4	57.2	103.1
	Mean	2.4 [4]	1.3	60.8 [4]	102.4
53	Ur.	4.7	1.4	202.0	371.7
	Chlor.	4.2	1.1	305.6	476.1
	SP	6.2	1.2	255.4	433.2
	Check	4.2	2.4	274.2	363.6
	Mean	4.9 [4]	1.5	259.3 [4]	411.2
73	Ur.	6.2	2.2		
	Chlor.	5.5	1.9		
	SP	6.7	2.6		
	Check	5.6	3.5		
	Mean	6.0 [4]	2.6		

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (1 per cent point) from the relevant control.

The trend in root rot through the season was toward a consistent increase with time. The rise was not great in the fallow plots but was quite large in the corn-vetch plots from the first to the second harvest; in percentage figures the increase over this period of 19 days was from an average of 8.0 to an average of 38.5 per cent. This increase will be discussed later.

As mentioned previously, the choice of corn and vetch was suggested by results at the University of Connecticut. It is not, obviously, possible to state with certainty whether the effect observed is to be ascribed to the corn or to the vetch. The vetch was seeded late and made relatively little growth before winter, while the corn of course had previously grown to maturity. The writer is of the opinion that the corn stubble was the important plant residue in this experiment.

B. Onion

Both at 56 and at 81 days from planting, the effect of a previous corn-vetch crop on onion was manifested by a slight increase in the amount of pink root discernible (Table 4). At the time of the earlier harvest, the incidence was low in all plots. The second harvest showed a more pronounced effect — approximately 10 per cent of the root area was involved in plants from plots previously in corn, while only about 3.5 per cent of the roots were affected in plants from the fallow plots. In both harvests, the difference between corn and fallow plots in root browning was significant at the 5 per cent point only.

TABLE 4

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON PINK ROOT AND YIELD OF ONION[1]

Harvest, days	Soil Treatment[2]	Root Grade[3]		Fresh Weight (grams per plant)	
		After Corn and Vetch	After Fallow	After Corn and Vetch	After Fallow
56	Ur.	0.8	0.2	36.0	56.2
	Chlor.	0.2	0.2	54.2	53.2
	SP	0.6	0.2	47.0	48.5
	Check	0.8	0.1	39.4	60.7
	Mean	0.6[4]	0.2	44.2	54.7
81	Ur.	2.7	1.4	49.9	91.4
	Chlor.	2.0	1.2	102.5	97.0
	SP	3.5	2.0	65.8	84.2
	Check	2.5	1.0	61.0	93.6
	Mean	2.7[4]	1.4	69.8[4]	91.6

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (5 per cent point) from the relevant control.

The yield (fresh weight of the entire plant) was not enough affected by corn to register a statistically significant difference. The data do show a generally lower average plant weight after corn than after fallow, but high variability in the experiment masked the significance of this effect. At the second onion harvest, there was evident a difference in weight in favor of the fallow plots, this difference being significant at the 5 per cent point.

Taken together, the data on onion suggest that there is a deleterious effect of corn on the following onion crop. This effect was demonstrated, at a low level of significance (5 per cent), in both harvests when the criterion of injury was pink root, and in the second harvest when injury was measured by reduction of plant weight. None of the three soil treatments caused significant changes in root browning or in plant weight.

Series II. The Effect of Timothy and Soybean on Root Rot

A. Head Lettuce

The effect of timothy on root rot of head lettuce is shown plainly in the first two harvests of this series (Table 5). In the first, at 36 days from transplanting, the average root damage in all soybean plots was 5.0 per cent, in all timothy plots 12.0 per cent. At 55 days the corresponding figures were 18.5 and 56.0 per cent. These differences were highly significant. In the third harvest, at 69 days, the root damage was still much more extensive in the timothy than in the soybean plots, but the difference was not statistically significant because of a markedly greater variability.

Turning to yield data, both harvests show that plant weights were much greater after soybean than after timothy. In the earlier harvest, the average plant weight was 78.4 gm. in the soybean plots, as against 50.9 in the timothy plots, a highly significant difference of more than 50 per cent. In the second harvest the same values were 327.6 gm. (after soybean) and 217.4 gm. (after timothy) — again a highly significant increase of about 50 per cent.

The only statistically significant effect of soil treatment on root rot in this series was found in the first harvest. Single degree of freedom analysis showed that there was a significant difference between the check plots and plots treated with chloropicrin, the latter having less root rot. Analysis within rotations indicates that this difference arose in large part from chloropicrin effects after timothy. In the timothy plots chloropicrin treatment reduced the average root damage from the check value of 21.0 per cent (grade 3.8) to 7.5 per cent (grade 2.3). It should be noted that the same trend, toward a reduction in root rot from chloropicrin treatment, was evident in the soybean plots, but the difference was not large enough to be significant. Since the significance of the effect of chloropicrin in the timothy plots was low (5 per cent), it is not possible to say that chloropicrin is associated with the crop residue effect. It will be brought out later that the evidence is in the other direction, in favor of the belief that the growth-promoting effects of chloropicrin are not related to crop residue effects.

TABLE 5

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON ROOT BROWNING AND YIELD OF HEAD LETTUCE [1]

		Root Grade [3]		Fresh Weight (grams per plant)	
Harvest, days	Soil Treatment [2]	After Timothy	After Soybean	After Timothy	After Soybean
36	Ur.	2.7	2.0	42.5	76.8
	Chlor.	2.3	1.2	66.3	85.1
	SP	3.4	2.1	47.6	83.0
	Check	3.8	2.1	47.3	68.6
	Mean	3.0 [4]	1.8	50.9 [4]	78.4
55	Ur.	6.1	4.0	166.5	263.9
	Chlor.	4.6	2.9	268.0	379.6
	SP	6.3	3.6	213.0	335.1
	Check	6.3	4.0	222.2	331.8
	Mean	5.8 [4]	3.6	217.4 [4]	327.6
69	Ur.	6.3	4.6		
	Chlor.	4.8	4.2		
	SP	5.9	4.8		
	Check	7.2	5.7		
	Mean	6.0	4.8		

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (1 per cent point) from the control.

Chloropicrin increased the fresh weight of lettuce both at 36 and at 55 days (Table 5). However, the differences were not statistically significant and, furthermore, seem to be independent of crop residue, i.e., the effect was almost as great after soybean as after timothy.

As in the case of lettuce after corn and vetch (Series I), this series also showed a significant increase in root rot with time. Unlike the earlier series, when per cent root rot is plotted against time the slope of the line is almost as steep in the "control" (soybean) plots as in the timothy. This time factor, and the relatively high level of root rot finally obtained in the soybean plots, will engage our attention later in this paper.

B. Spinach

The effect of a preceding timothy crop on root damage is again demonstrated in the data from the first harvest of spinach plots (Table 6). The average root area browned was 4.0 per cent in all soybean plots, 7.5 per cent in all timothy plots, the difference being highly significant.

TABLE 6

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON ROOT BROWNING AND YIELD OF SPINACH [1]

		Root Grade [3]		Fresh Weight (grams per plant)	
Harvest, days	Soil Treatment [2]	After Timothy	After Soybean	After Timothy	After Soybean
49	Ur.	2.5	1.9	30.8	45.4
	Chlor.	1.6	1.3	37.6	38.8
	SP	2.9	1.4	40.9	45.5
	Check	2.3	1.8	42.7	37.3
	Mean	2.3 [4]	1.6	38.0	**41.7**
67	Ur.	3.8	3.4		
	Chlor.	2.2	1.8		
	SP	2.9	3.2		
	Check	3.6	2.7		
	Mean	3.1	2.8		

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (1 per cent point) from the control.

The later harvest, at 67 days from planting, presents a different picture. There was no longer any significant effect of the previous crop, although the average incidence of root damage was somewhat higher (up to 13 per cent). This is an example of the tendency of previous crop effects to disappear during the season.

Yield data were taken only for the first harvest (49 days). The data do not show any significant difference attributable either to previous crop or to soil treatment. The more extensive root damage noted above following timothy was, obviously, not reflected in growth. This was not unexpected, in view of the low average incidence of root damage in even the most severely affected plots.

Analysis of data on root damage shows a significant soil treatment effect in both harvests. Comparison of treatment means indicates that this is to be attributed exclusively to chloropicrin. Treatment with chloropicrin reduced root browning in both harvests. In contrast to the results with potato, there is evidently some association of the chloropicrin effect with timothy; the statistical evidence for this association is, however, of a low order of significance (5 per cent point) and applies only to the second harvest, in which there was no significant effect of the previous crop *per se*. In the first harvest there was no association of chloropicrin effects with previous crop effects, i.e., the reduction in root damage attributable to chloropicrin is approximately the same after soybean as after timothy. Taken as a whole, there is no good evidence that chloropicrin antidotes the timothy effect.

C. Potato

Only root browning data were collected in this series because of the difficulty of ensuring accuracy in weighing plants. The data from the first harvest (Table 7), at 60 days from planting, show that the previous crop of timothy caused a highly significant increase in root damage over a soybean crop, there being approximately twice as much root injury in the former as in the latter case. The injury was not, however, in any case very high, a maximum of 4.5 per cent of the root length being browned. How significant such an effect might be in practice is difficult to decide. In the second harvest, at 84 days, there was no difference between the two crop residues, and the general level of root injury had increased to about 11.3 per cent (grade 3.3). Damage of this extent is probably of practical importance, but the design of the experiment does not offer information on the cause of the root injury.

In both potato harvests, analysis of variance allocates a highly significant effect to soil treatments. Comparison of treatment and control means was therefore carried out. In the first harvest, this comparison showed that root injury was significantly lower in plots treated with chloropicrin and significantly higher in plots receiving Uramon, than in the check plots. These treatment effects were independent of the previous crop, i.e., occurred both after soybean and after timothy. Inspection of the data suggests that both treatment effects are, if anything, greater in the soybean than in the timothy plots, but statistical analysis does not offer evidence on this point.

In the second harvest, the Uramon effect was no longer significant, although root injury was somewhat greater in the treated plots than in the checks. The chloropicrin effect was, however, still significant, i.e., chloropicrin caused a reduction in root injury. Comparison of treatment means confirms the trend noted in the first harvest: the effect of chloropicrin was greater in the soybean plots than in the timothy plots. In this harvest the statistical analysis supports the conclusion that there is in fact a significant chloropicrin effect only after soybean, the reduction after timothy not being significant.

TABLE 7

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON ROOT BROWNING OF POTATO [1]

Harvest, days	Soil Treatment [2]	Root Grade [3] After Timothy	After Soybean	Treatment Mean
60	Ur.	1.3	0.7	1.0 [4]
	Chlor.	0.6	0.2	0.4 [4]
	SP	1.1	0.7	0.9
	Check	0.9	0.4	0.6
	Mean	1.0 [4]	0.5	
84	Ur.	4.6	4.0	4.3
	Chlor.	2.1	1.4	1.8 [4]
	SP	3.9	3.6	3.8
	Check	3.5	3.4	3.4
	Mean	3.5	3.1	

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (1 per cent point) from relevant control.

Evidently, root damage in potato may be increased by a particular crop residue (e.g., timothy) or decreased by soil treatment (e.g., chloropicrin), but the relation of these two effects is not one of simple opposition. An experimental design which will isolate these factors, perhaps by using fallowed land as one of the controls, is necessary before their relations can be made clear.

Series III. The Effect of Clover and Soybean on Root Rot

Leaf lettuce grown after clover evinced a consistently higher incidence of root injury and a lower fresh weight than control plots following soybean. In the first harvest, at 42 days from planting (Table 8), root browning in all clover plots averaged about 17 per cent (grade 3.5), while in all soybean plots the average was 7 per cent (grade 2.2). The difference was highly significant. The same trend was shown in the second harvest, but the difference was less and its significance lower (5 per cent point).

Plant weights of lettuce after clover and soybean show a similarly unfavorable effect of the former at both harvest dates. The average plant weight in all soybean plots was about 50 per cent greater in

TABLE 8

THE EFFECT OF PREVIOUS CROPS AND SOIL TREATMENTS ON ROOT BROWNING AND YIELD OF LEAF LETTUCE [1]

Harvest, days	Soil Treatment [2]	Root Grade [3]		Fresh Weight (grams per plant)	
		After Clover	After Soybean	After Clover	After Soybean
42	Ur.	3.4	2.4	13.6	20.8
	Chlor.	3.2	2.0	25.1	30.7
	SP	3.6	2.6	15.3	22.3
	Check	3.6	1.8	13.2	22.3
	Mean	3.5 [4]	2.2	16.8 [5]	24.0
53	Ur.	4.6	2.1	56.7	86.0
	Chlor.	2.4	2.6	63.8	114.3
	SP	3.8	3.4	59.4	72.8
	Check	3.9	3.0	55.8	86.1
	Mean	3.7 [5]	2.8	59.0 [4]	89.8

1. Each entry in the table is the average of four replicate plots.
2. Ur. = Uramon; Chlor. = Chloropicrin; SP = Superphosphate.
3. See text (p. 11) for method of grading roots.
4. Differs significantly (1 per cent point) from the control.
5. Differs significantly (5 per cent point) from the control.

both harvests than that in the clover plots, although over-all variability reduced the significance of these differences to the 5 per cent level.

The several soil treatments in this series were in no case responsible for statistically significant effects. Inspection of the weight data suggests one treatment effect: in both harvests and after both clover and soybean, the plant weights were highest in chloropicrin-treated plots. The increase in average weight over the check ranges from about 15 to almost 100 per cent. Since this effect is equally evident in the clover and soybean plots, it is not related, at least directly, to the root damage factor.

In comparing this with other lettuce series, it must be borne in mind that this was planted 53 days later than the others. Since it is likely that any effect of a preceding crop is dissipated gradually during the growing season, it is not surprising that the effects on a late-planted crop should be less than on one planted earlier. The increase in root rot between harvests was insignificant, suggesting that the residue had decomposed to a considerable extent.

The Effect of Time on the Development of Root Rot

One of the most striking regularities in these data is that almost all plots, regardless of plant residue or chemical soil treatment, increased in root rot through the season. In the head lettuce experiments — lettuce after corn and vetch (Table 3) and lettuce after timothy (Table 5) — the rate of increase through the season was apparently greater in the treated than in the control (fallow or soybean, respectively) plots. A graph of disease grade against time of harvest in these two experiments shows that the slope of the line representing the rate of increase of root rot is at least 20 per cent greater in the treated than in the control plots.

Data on onion (Table 4), spinach (Table 6), potato (Table 7) and leaf lettuce (Table 8) show an increase of disease throughout the season but, unlike the head lettuce plots, the rate of increase is not much affected by the plant residue present.

These relations must be studied in the light of the experimental design, which was not planned to yield statistically valid conclusions on the time factor. Two limitations in particular exist. First, the several harvests were taken systematically in each ultimate subdivision of the field, i.e., analysis of variance cannot be used to test the significance of differences. Second, at most only three, and in some cases only two, harvests were made.

Bearing these considerations in mind, it is nevertheless of importance to study the time factor in some detail. While the data will not always permit of definite positive conclusions, there are some hypotheses which can be ruled out as highly improbable.

Consider first the hypothesis that residues act as a pure chemical toxicant, uncomplicated by biotic factors. Assuming no deterioration or inactivation of the chemical and no change in cell or tissue resistance to it, this hypothesis would offer no means of explaining an increase in root rot with time, such as actually occurred. The hypothesis also would leave unexplained the occurrence of root rot in plots fallowed the previous year.

A second hypothesis, subsidiary to the above, might be constructed with the addition of the not unreasonable postulate that the active chemical factor decomposed at a finite rate. Under these conditions, disease should decrease with time, since new growth would be exposed to a constantly decreasing concentration of the hypothetical chemical.

Obviously, neither of the above hypotheses fits the facts in the head lettuce experiments. It is necessary to postulate further that biotic factors, capable of increase in amount with time, are involved in the etiology. And it is at this point that the data fail to provide a definitive choice between or among alternatives.

One such alternative explanation is that the residue in question increases root damage by providing a favorable environment for a living pathogen, which is, however, also able to subsist in the control plots. Such a hypothesis would explain, formally at least, the data on the effect of time. Differing slopes would then represent perhaps different portions of the exponential curve of increase of a population of pathogens.

However, the data on the time factor are equally consistent with a different explanation: that there is in any soil a population of saprophytic organisms, which can attack plants only by way of injuries. The effect of deleterious residues could then be viewed as a special case of injury, occurring early or late in the season and superposed on "normal" injuries (growth cracks, insect damage, and tillage injury), which latter are responsible for root damage in the controls. The slightly greater magnitude of the slope of the disease-time graph would, on this hypothesis, be an expression of the increase of a population of saprophytes or low-grade parasites in the rhizosphere or adjacent soil. That is, as suggested above, the experiment is measuring different portions of an exponential growth curve.

An experiment of a different design is clearly necessary to decide these questions. The present data do appear to rule out a simple chemical mechanism of plant residue effects, such as served to explain laboratory data on root injury (6). In the earlier experiments the active material disappeared with time, as would be expected, and the experimental design eliminated possible biotic factors.

Greenhouse experiments (Table 2) are closer to the laboratory than to the field experience, in that soil-residue mixtures incubated at high temperature and moisture and without any plants lost their toxicity in a short time. To get comparable field data, it would be necessary to make successive plantings of a test crop in the same soil-residue plot. Absence of the susceptible plant would presumably prevent the building up of a population of pathogens.

The Effect of Superphosphate and Nitrogen on Root Rot

Applications of a nitrogenous fertilizer were made, as stated earlier, to eliminate, if possible, the common effect of high-carbon residues in causing a nitrogen deficiency. In no single case did heavy application of Uramon decrease root damage associated with plant residues. The only significant effect, in fact, was that potatoes treated with Uramon showed at the first harvest actually higher levels of root damage than did untreated controls. The conclusion seems justified that nitrogen depletion was not a factor in the plant residue damage observed.

Liberal application of superphosphate similarly had no discernible effect on the residue phenomenon. Failure to increase yield or to decrease root rot may be taken as evidence that the field level of phosphate was not a limiting factor.

The Effect of Chloropicrin on Root Rot

Chloropicrin was the only one of the three soil treatments tested which exerted a more or less consistent influence on the results. In the first series (Table 3), involving the effect of a corn-vetch crop on head lettuce, second-harvest yields were increased significantly by the fumigant in the fallow plots, not in the corn-vetch plots. Since the latter showed significantly lower yield and higher root rot than the former, it is clear that chloropicrin did not antagonize plant residue toxicity. Chloropicrin treatment of leaf lettuce soil after soybean and clover had a tendency (not statistically significant) to increase yields after both cover crops (Table 8). The same was true of head lettuce after timothy and soybean (Table 5). In the last-named series, root rot data from the first harvest show a barely significant effect of chloropicrin in reducing the root damage after timothy; after soybean, the trend was the same but the difference in favor of chloropicrin was not significant. There was no influence of chloropicrin on pink root or yield of onion.

Perhaps the clearest chloropicrin effects are found in the data on potato and spinach. Chloropicrin reduced root damage significantly in both these crops at both harvests (Tables 6 and 7), but there was no association with previous crops. In both cases root rot was increased by a previous crop of timothy, but the reduction in root rot caused by chloropicrin was "across the board".

It may be concluded that, while chloropicrin reduces root rot, its action is not related to the crop residue effects demonstrated in the same field experiment. It is possible to speculate that the fumigant controlled a mild infestation of some pathogenic organism which was distributed at random throughout the field.

Possible effects of chloropicrin on the nitrogen factor are unlikely. The additional nitrogen in 545 lb. per acre of chloropicrin amounts only to about 46 lb. per acre of nitrogen; Uramon at a much higher level, as already indicated, had no effect. Stark *et al* (40) demonstrated that chloropicrin at the usual dosages has no discernible effect on the nitrifying and ammonifying bacteria in soils, so that treatment with it is unlikely to have altered the form of the soil nitrogen significantly.

The results of the chloropicrin treatment have a direct bearing on the possible role of nematodes in the field experiment. The data do not allow us to allocate the observed effect of chloropicrin to a specific factor but they do permit a negative conclusion to be drawn: since the effect of previous crops is not related to chloropicrin effects, i.e., since the action of the fumigant is exerted without regard to the previous crop, the previous crop effect is not related to nematode injury. Put another way, if we assume that the chloropicrin dosage used was adequate for nematode control, then its failure in the preponderance of cases to neutralize the influence of a previous crop indicates that nematodes are not responsible for the crop residue effect.

No examination of plants or soil for nematodes was undertaken in these experiments. The type of injury observed, however, was not at all similar to that described by Jenkins (21, 22) as resulting from the attack of the meadow nematode on cereals and tobacco. In particular, the lesions described by Jenkins were much smaller than those reported here.

Final disposition of this question of the possible association of nematodes with the previous crop effect can undoubtedly be made in an experiment designed for the purpose. In the, at present, unlikely event that nematodes are indeed the active agent, the practical significance of the previous crop effect would be unchanged.

The Relation of Root Damage to Yield

Inspection of the field data (Tables 3-8) and plotting of scatter diagrams (mean fresh weight against mean root grade) indicate that in most of the experiments a high root damage grade was associated with a lowered fresh weight per plant. This was true of lettuce and onion after corn and vetch (Tables 3 and 4), of lettuce after timothy (Table 5), and of leaf lettuce after clover (Table 8). The pronounced negative regression suggests that the root damage was the cause of the decreased plant size.

In the one exception to this rule, spinach after timothy (Table 6), the extent of root rot was low and the timothy effect on it was significant only in the first harvest. In this case either the imprecisions of the fresh weight method were great enough to conceal any diminution caused by root rot, or the damage to the root system was not a limiting factor in plant growth.

DISCUSSION

Previous work at this Station on the root rot problem (6, 17) had been confined to laboratory experiments which, however convincing in themselves, cannot be evaluated properly without corroboration from field experience. As an example of failure of correlation between laboratory and field toxicity studies, recent work on guayule may be cited. Bonner and Galston (5) found that root excretions of guayule are toxic to the same plant in solution culture, and identified one of the two active materials as *trans* cinnamic acid. Later studies with guayule plants in soil (4) confirmed the toxicity of *trans* cinnamic acid but soils in which guayule had grown for as long as 8 years supported as good growth of guayule as did any soil tested.

Laboratory studies (6), using a quick assay based on the browning of seedling radish roots, demonstrated that water extracts of ladino clover and ryegrass contain toxic materials, that soybean extracts are not toxic, and that corn extracts are so only under special conditions. It was further shown that decomposition of the plant residues results in progressive loss of toxicity. The first problem, therefore, in discussing the data of this paper, is to see in what degree, if any, field experience corroborates and validates the laboratory work. Later, it will be necessary to consider possible alternative hypotheses which may offer a simpler or more orthodox explanation of the data than the hypothesis of chemical injury previously advanced.

The fact of damage by plant residues, whatever the mechanism, is demonstrated in both greenhouse and field experiments. In the field, the most pronounced effect was observed when lettuce was used as the test crop. Taking first the data on growth of head lettuce after corn and vetch as compared to its growth after bare fallow (Table 3), there is evident a highly significant effect at all harvest dates of corn over fallow, both as regards root damage and yield. For example, in the last harvest in this series there was over six times as much root damage after corn and vetch as after fallow; in the second harvest the average fresh weight of plants in the corn plots was only 63 per cent of that in fallow plots. These differences are large enough to be of practical significance to the grower.

Less striking but still significant results of the same sort were obtained with a late crop of leaf lettuce after clover and soybean (Table 8). The possible significance of the smaller magnitude of this effect has already been considered.

A similarly adverse effect on root condition and yield of head lettuce was noted in timothy plots, when compared to soybean as a previous crop (Table 5). The yield difference was high enough to be of practical importance, while root damage in the first two harvests was more than twice as great following timothy as following soybean. In the third harvest of this series there was no significant difference between timothy and soybean. In part, failure to attain significance can be attributed to the variability within treatments, but there is another factor. By the third harvest (69 days from transplantation) lettuce after soybean developed considerable root damage, ranging in individual plots from grade 1.8 (5.0 per cent damage) to grade 8.4 (91.0 per cent), and averaging grade 4.8 (37.0 per cent). There being in this series no fallow control, we are not able to say definitely that soybean (and weed) residues caused this damage, but it is a distinct possibility. In the first series, which occupied part of the same field and was planted the same day with plants from the same bed, lettuce after bare fallow in the third harvest (73 days) averaged only grade 2.6 (9.0 per cent) root damage (Table 3). The experimental design does not permit of a direct comparison between series, but the fourfold difference between nearby soybean and fallow plots suggests strongly that soybean residues are not entirely innocuous to lettuce.

Onion after corn and vetch (Table 4) showed significantly more pink root than after fallow, but the difference was not great, and no effect on yield was discernible. By contrast, in experimental plots at the Storrs Agricultural Experiment Station, onion proved to be extremely sensitive to a previous corn-vetch succession. Evidently factors of location and soil type are of importance. Results at New Haven, however, are at least suggestive in relation to the etiology of pink root; the data justify an investigation into the role of microorganisms, primary pathogens or secondary invaders, in this disease.

The timothy effect was demonstrable in an early-season harvest of spinach, not at a later harvest (Table 6). While the effect of the previous timothy crop on root browning was highly significant, yield effects could not be discerned.

Finally, the timothy effect on root browning was evident when potato was used as the test crop (Table 7), although again the difference between soybean and timothy was not great and the highest level of root damage was much less than that commonly found in, for example, the lettuce experiments.

Field and greenhouse data reported here do, therefore, corroborate the previous laboratory studies in that injury to roots can be detected in media containing certain crop residues. Comparison of particular crop residues in the two types of experiments is less close, in the first place because the same residues were not used uniformly, and in the second place because different test plants were employed. Both in laboratory and field, clover caused injury (ladino clover in the former, red clover in the latter). In both, again, soybean residues were relatively non-toxic. Timothy, injurious in the field to spinach, lettuce, and potato, was not tested in the laboratory. Corn stover was in most cases not injurious in the laboratory to radish seedling roots, while in greenhouse studies the same residues in soil caused detectable root browning in lettuce transplants. In the field, the plots containing plowed-under corn stubble and vetch exhibited marked damage to lettuce. The case of corn, therefore, marks a failure of correlation between the laboratory assay and soil studies. In this connection, it may be recalled that Garner, Lunn, and Brown (15) found corn roots but not corn stover (tops) injurious to tobacco in soil; the corn roots were applied to soil at the rate of 2.5 grams per 100 grams of soil. It should also be borne in mind that the laboratory results showed that corn during decomposition under conditions of limited oxygen supply developed transitory materials which were toxic to radish.

In the literature on crop residue effects there is no body of data comparable to the field experiments reported here. Disregarding for the moment the criterion of injury and the explanation offered by the authors, survey of the literature shows that timothy as a previous crop favors the appearance of brown root rot of tobacco in the field (23, 24, 42); L. T. Richardson (35) found timothy residues to favor the damping-off of tomato by *Phytophthora parasitica*. Other grasses claimed to exert unfavorable effects on later crops include bromegrass (3, 29), cereal straw (8, 9, 46), and rye (12, 27, 34). The injurious effects of clovers reported in the present work may be compared with the effect of sweet clover on sugar beet stands (11), of red clover on strawberry and tobacco growth (17), of red clover on tobacco brown root rot (23), and of the same crop on corn root rot (34). Finally, corn stubble or corn roots have been reported to increase tobacco brown root rot (15, 23, 48). Miscellaneous plant materials that have been found injurious to growth of the same or other species include lespedeza and some weeds (26), peach root bark (32), and sorghum (38); in the last-named case, later workers (30) believe the injury to result from nutrient and moisture depletion by sorghum.

In these experiments the effect of plant residues on root rot was not a result of deficiencies in either nitrogen or phosphorus. Addition of large amounts of these elements to the soil had no effect on the phenomenon studied.

By indirect evidence (the failure of chloropicrin to reduce the root rot associated with plant residues) the causative role of nematodes in the field experiments is rendered very unlikely. Direct studies of the nematode factor, however, would afford more certain evidence. It is, for example, possible that chloropicrin as used was not effective against a nematode; although unlikely, this avenue should be explored.

Some new light has been thrown on the growth-promoting effect of chloropicrin treatment by this work. The effect was observed, and it was further noted that in many cases chloropicrin caused reductions in root rot. Neither increase in yield nor decrease in root damage was ever associated with plant residue effects. Usually residue plots and control plots both showed the favorable influence of the fumigant if either did. Tentatively, it seems likely that the fumigant reduced root damage of some type other than that induced by plant residues. This reduction in root damage, possibly nematode-induced but not associated with previous crops, might be the explanation for the higher yield attributable to chloropicrin.

The over-all significance of the results of these experiments may be difficult to assess at this stage of our knowledge, but some conclusions do emerge. It should be emphasized first that the value of soil organic matter as such, established by agronomic research of the last 50 years or more, is not thrown into question. The experimental design was not meant to test the validity of the prevalent theories of the role of organic matter in soil fertility and productivity.

The data do most emphatically, however, raise the question of the kind of organic matter and the time of its application. No one would argue that corn and vetch residues in this experiment were beneficial to the growth of lettuce; on the other hand, onion suffered relatively little. For the grower concerned with maintaining the permanent value of his land by conserving organic matter, the slight damage to onion might not be too high a price, but the grower of head lettuce is not apt to be able to afford the losses suffered in retaining a rotation involving corn before lettuce.

For any given soil type and locality it seems clear that certain crops cannot be successively planted without severe losses from root rot in the second crop. Care in the choice of the preceding crop and especially in the allowance of time for decomposition is necessary. The importance of the soil type and locality has been touched upon before in a qualitative comparison of the effect of corn and vetch residues on onion at Storrs and at New Haven. It is to be expected that such differences will be found elsewhere as well.

As this paper was being prepared for publication the report of McCalla and Duley (28) appeared. In connection with studies on the stubble-mulch system of corn culture, these authors found that water extracts of sweet clover contain a potent inhibitor for seed germination and seedling growth. While field experience does not as yet indicate any discernible depressant effect of a sweet clover mulch on corn, McCalla and Duley point out the obvious practical bearing of such germination inhibitors in plant residues.

The field experiments reported in the present paper were designed to test an hypothesis derived from laboratory studies of a more or less artificial system. Very briefly, the hypothesis is that chemicals in undecomposed plant residues may affect plant growth adversely through killing of root cells. Evidence in favor of the hypothesis has been presented, and the field data are not at all inconsistent with it. They do not, and were not intended to, provide all of the evidence, e.g., no attempt has been made in field experiments to assess the possible role of the biotic factor. The earlier laboratory experiments eliminated this factor and it was not further considered. Unless the field data agree with the laboratory data only by coincidence, the hypothesis of initial chemical injury by plant residues is supported by both lines of work. The progressive increase in root rot with time in the field experiment suggests that secondary biotic factors are involved. Final proof will presumably come only with isolation and identification of the active substance or substances, disproof only with the establishment of a more probable mechanism for the undoubted effect which has been observed.

The biotic element, particularly the microflora of the soil and the rhizosphere, very likely plays a part in the plant residue effect. It is not enough, however, to postulate some undefined "disequilibrium" as an explanation of the phenomenon. Such explanations not supported by careful microbiological analysis, are not explanations at all; they merely add a new and possibly unnecessary link in the chain of causation. Nor will evidence of the role of microorganisms in nature be obtained by plating soil samples on media designed for human pathogens and studying the isolates by means of physiological reactions developed for the differentiation of organisms of medical or industrial importance. It is becoming increasingly clear that the predominant soil microorganisms escape us almost completely when we use these methods only. The work of Conn and Darrow (10) and of Topping (43, 44) on the soil microflora provides an indication of the true nature of this population of organisms. The studies undertaken recently by a group of Canadian workers (51) may lead to a much clearer understanding of the relationships existing among microorganisms, dead organic matter, and the living cells of the plant root.

SUMMARY

The experimental evidence presented supports the hypothesis that certain plant residues cause an increase in root rot and a decrease in yield of succeeding crops. The effect is not explicable on the basis of nutrient starvation nor on the grounds of simple pathogenesis by a nematode or microorganism. Rather, the data permit the conclusion that plant residues in the soil exert a direct toxic effect on the roots of susceptible plants, probably complicated by the action of secondary rot-producing microorganisms.

In the greenhouse, addition of corn stover to soil caused root rot in lettuce transplants and a concomitant lowering of growth. Residues allowed to decompose for 30 days at high temperature and moisture were no longer injurious.

In field experiments head lettuce after sweet corn and vetch was severely injured, the damage appearing both in root rot observations and as decreases in yield. As high as 60 per cent of the root area was discolored, and the diminution in yield (fresh weight) was as high as 40 per cent.

Leaf lettuce after a previous crop of clover was similarly affected, when compared to the same crop after soybean (and weeds). Root rot attributable to the clover residues reached an average level of 19.5 per cent, as compared to 10.5 per cent after soybean. The average plant weight of lettuce after clover was about two-thirds of that in the soybean controls.

A previous cropping with corn and vetch increased pink root of onion slightly but significantly, while having no significant effect on yield.

Head lettuce was also affected by timothy residues: root rot ranged as high as 60 per cent, and the average plant weight was about 67 per cent of that following soybean.

In an early-season harvest, spinach root rot was increased by timothy residues, but in a later harvest there was no difference between timothy and soybean plots. Yield was not affected.

Timothy residues similarly caused a small but significant increase in root browning of potato in an early-season harvest. The effect was not significant at later harvests.

Fertilization with supplemental nitrogen or superphosphate had no influence on the previous crop effect. It is, therefore, concluded that the mechanism of injury is not merely an unavailability of nitrogen or phosphorus.

Soil treatment with chloropicrin resulted in significant increases in yield and reductions in root rot of lettuce, spinach and potato. However, the stimulating effect of chloropicrin could not be attributed to any correction by the fumigant of residue damage, since the effect of chloropicrin was usually as great on control plots as on plots containing injurious residues. Failure of chloropicrin, a nematocide, to reduce the plant residue effect is believed to indicate that nematodes are not concerned. The possible nature of chloropicrin stimulation of plant growth is discussed briefly.

The observed injurious effect of certain crop residues is in no way an argument against the principle that an adequate level of organic matter should be maintained in the soil. The results do, however, raise the question of the kind of organic matter to be applied and the time of such application. For any given soil type and locality there are some crops which will be depressed in growth and will have a high level of root rot when they are planted in soil containing undecomposed or only partially decomposed residues of other crops.

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