UNITED STATES DEPARTMENT OF AGRICULTURE

In Cooperation with the
Wisconsin, Connecticut, and Massachusetts Agricultural
Experiment Stations

DEPARTMENT BULLETIN No. 1410

Washington, D. C. ▼ July, 1926

THE BROWN ROOT ROT OF TOBACCO AND OTHER PLANTS

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INTRODUCTION

During the last 10 years a disease of tobacco which is characterized by brown and decayed roots has been under observation and the subject of considerable experimental work. This condition has been referred to as brown root rot, to distinguish it from the more generally known black root rot due to *Thielavia basicola* (B. and Br.) Zopf. Intensive studies along etiological lines have failed to yield conclusive evidence as to the actual cause of the disease. Although most of the evidence points to a parasitic origin, other evidence apparently is contradictory to a parasitic hypothesis. The observations over a period of several years, together with the results from rotation experiments reported in this bulletin, show that the occurrence of brown root rot is closely correlated with the preceding crops grown on the land. Tobacco grown on sod is commonly most markedly affected, and the use of winter cover crops may bring on a similar condition. From an agronomic standpoint as well the problem becomes very complex, since the kind of preceding crop, the soil type, the environmental conditions, and other circumstances determine the occurrence and the severity of the disease.

So far as is known, brown root rot is most prevalent in the tobacco soils of the Connecticut Valley. A similar condition is known to exist in Wisconsin, Maryland, Kentucky, and in several other tobacco-growing districts, but in the absence of a known parasite or other causal agency it is not readily demonstrable that the conditions observed are all due to the same cause.

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Other plants are affected by brown root rot, notably the tomato. Potatoes are affected to a lesser extent, as are many legumes. Little is known relative to the importance of this disease in the culture of other crops. In the case of tobacco culture in New England, however, it is to be ranked as one of the major maladies affecting the crop.

The experimental work reported in this bulletin has been mainly conducted in the laboratories at the Wisconsin Agricultural Experiment Station, using soils from the Connecticut Valley, but the field plats were located in the Connecticut Valley. The results therefore apply more specifically to the soils of that valley, although in practice the conclusions are believed to have a wide application in tobacco culture.

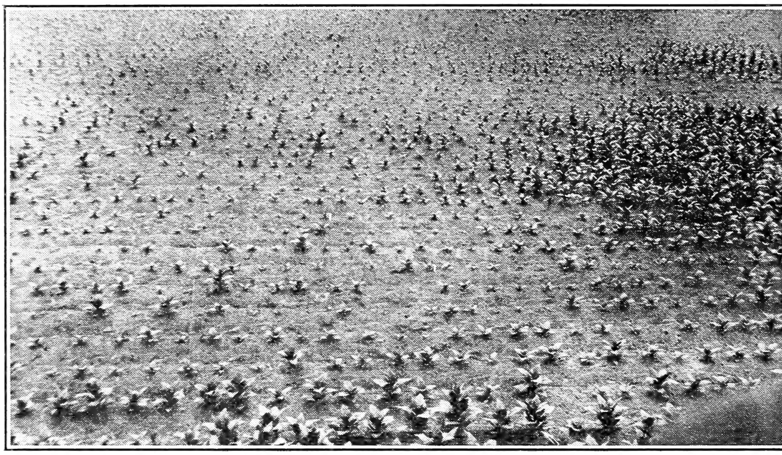

FIG. 1.—A field of Havana tobacco grown at Suffield, Conn., showing a crop which is practically a failure, due largely to brown root rot. Note that some spots in the field are less seriously affected

SYMPTOMS OF BROWN ROOT ROT

Brown root rot occurs both in the shade-grown and sun-grown tobacco in the Connecticut Valley. Three varieties are here involved—the shade-grown Cuban, the Havana Seed (Connecticut Havana), and the Connecticut Broadleaf, the latter two varieties being grown in the open field. The aboveground symptoms may vary somewhat with the different varieties and conditions. The most striking aboveground symptoms are the general stunting (fig. 1) and the temporary wilting of the affected plants during periods of high transpiration. The most striking cases of wilting have been observed in the Havana variety grown in the open field (fig. 2), although this may be equally common in the Broadleaf variety in New England. The shade-grown tobacco is not ordinarily so subject to wilting, apparently on account of the reduced transpiration under such cultural conditions. Under some conditions a gradual yellowing and death of the lower leaves of the plant occur, particularly during the late summer. The stunting, wilting, and yellowing are also characteristic of the Thielavia root rot and may, of course, be caused by any other agency or condition interfering with the food or water supply of the plant.

The symptoms on the root system are more characteristic. Where the disease is extensive the plant is easily pulled from the soil, and the few remaining roots on the base of the stalk are brown and decayed; or, as is frequently characteristic in moderately stunted plants later in the season, a considerable number of well-developed roots with distinct lesions may be present in the uppermost layer of soil, but the taproot and strong secondary roots normally present in the deeper layers of soil are either lacking or have made little or no growth. These conditions might be mistaken for Thielavia root rot except for the absence of black lesions and spores of Thielavia. (Fig. 3.) Their absence in the presence of a root decay is one of the principal diagnostic characters for brown root rot. In both

FIG. 2.—A diseased field of Havana tobacco at Deerfield, Mass., showing characteristic wilting as a result of a deficient root system. The symptoms on the roots were typical of brown root rot

diseases the plants are apparently stimulated to send out more new roots than would otherwise develop from the portion of the stalk below the surface of the soil. These may or may not make considerable headway into the soil before being destroyed. The roots which are able to persist are on the average generally nearer the surface than the main fibrous roots of a normal plant.

So far as known the plants never actually die as a result of brown root rot but may remain throughout the entire season without making much growth. On the other hand, they may show a decided tendency to recover late in the season.

Brown root rot is not ordinarily distributed uniformly over large field areas. So far as observation has gone, the disease in its most serious form is often more or less limited to spots in the field; at other times, the whole field may be very uniformly affected except for occasional small spots of good tobacco. The lack of uniformity of the plants is characteristic in fields after sod land in Wisconsin. Often the back furrow in a field is the only place where the tobacco grows normally. (Fig. 4.)

HISTORICAL REVIEW

So far as could be ascertained, the disease now referred to here as brown root rot of tobacco was undescribed at the time these studies were undertaken in 1915. One of the writers reported the occurrence of the trouble in 1919[1] (*11*). At that time it was believed that Fusarium might be the causal organism, since apparent mild infection was sometimes obtained with certain strains isolated from diseased hosts, although no heavy infection comparable to that occurring in the field was ever found. Clinton (*4*) in 1920 described a red root rot of tobacco in the Connecticut Valley which is undoubtedly the same as our brown root rot. Although red roots occasionally occur in this disease, it is believed that " brown root rot " is a better descriptive name than " red root rot." Chapman (*3*) in 1920 also discussed the root-rot situation in the Connecticut Valley and recognized a new disease distinct from black root rot. Neither of these writers, however, showed that any particular organism was definitely associated with the disease.

FIG. 3.—Lesions of brown root rot on roots of tobacco (*A*) and tomato (*B*). The dark-colored lesions shown here are actually brown rather than black. The localized lesions seem to bear a close relation to the point of attachment of secondary roots

In 1924 the senior writer briefly described the disease in a general treatise on tobacco diseases (*12*).

Whether or not this disease has been described on crops other than tobacco can not be definitely ascertained. Occasional references in literature are to be found to obscure root diseases of various plants, attributed to Fusaria, Rhizoctonia, or other organisms, where the causal agency has not been definitely established.

The western tomato blight, for instance, ascribed by Humphrey (*9*) to Fusarium and by Heald (*7*) to Rhizoctonia, has some simi-

[1] The serial numbers in italic in parentheses refer to " Literature cited," at the end of this bulletin.

larity to brown root rot as it occurs on tomatoes in the writers' experiments. Byars and Gilbert (*2*) also report a Rhizoctonia disease on tomato which resembles brown root rot of tobacco. These authors apparently based the Rhizoctonia relation, however, on microscopic examination only.

If examined from an agronomic point of view, it may be found that we are dealing with an old problem under a new name. One of the earliest scientific explanations of reduced soil fertility was based on the development of toxins in the soil, resulting either directly from excretions of the living roots or from the products of decomposition of the preceding crops.

This subject has been the ground for considerable controversy, and whether or not toxins actually exist in field soils can not be regarded as an established fact. Nevertheless, the results of several investigators, from those of Macaire (*14*), as early as 1832,

FIG. 4.—A field of tobacco following timothy sod near Cambridge, Wis. The single row of large plants follows a backfurrow, the treatment otherwise being the same as in other rows

to the recent work of Garner, Lunn, and Brown (*5*), establish beyond any reasonable doubt that crops often affect the yield of succeeding crops deleteriously to a marked degree.

This subject has so recently been reviewed by Garner and his associates (*5*) that the reader is referred to the publication cited, which is, moreover, closely related to the present bulletin, since its senior author was able to observe the experimental plats at Upper Marlboro, Md., during several seasons and to experiment with soil samples from those plats. Studies on these soils seem to justify the belief that in the broadest sense the problem in Maryland is essentially similar to that described in this bulletin. The symptoms of brown root rot were not nearly so evident in Maryland as in the Connecticut Valley, but it is believed that the condition referred to as brown root rot played some part at least in the experimental results obtained at Upper Marlboro.

The extensive experiments of Garner and his associates show that the tobacco plant is particularly sensitive to the effects of certain preceding crops used as winter soiling crops or in rotation with tobacco. According to their results, the limited use of soil-improving crops under favorable circumstances may prove profitable, but conditions may easily arise where their use is positively detrimental to tobacco. Similar effects are shown to occur on potatoes and corn following certain legumes and nonlegumes in rotation, with the exception that corn and small grains have been generally benefited by legumes in rotation. The evidence presented that these results can not be attributed to any known soil-borne disease or to plant-food relations is convincing.

Mention should be made of other workers who have noted similar results with tobacco and other crops. Among these, Bedford and Pickering (*1*), Howard and Howard (*8*), and Hartwell and his associates (*6*), particularly, have shown cases of the harmful effect of one crop upon another where the effect was presumably not pathological in its nature. There is no general agreement among these investigators, however, as to the nature of the deleterious agency in these crop effects.

ISOLATIONS FROM DISEASED ROOTS

It is not proposed to present in detail the results of a large number of isolations made from diseased roots and the inoculations performed with the organisms obtained, since the results on the whole are inconclusive, if not entirely negative.

Most of the isolations have been made from plants grown in the greenhouse in affected soil, although many of the specimens used for that purpose came directly from the field. Small pieces of the roots with lesions in varying stages of development were washed in several changes of sterile water and plated out on potato agar, usually acidified with lactic acid when fungous development was desired.

The platings have been made mainly from tobacco grown in soil from two different fields in the Connecticut Valley and from one field in Maryland.

One series of records of these isolations shows that 505 fragments were plated out and that growth of a species of Fusarium was obtained from 329 fragments, or 65 per cent of the lesions. The abundant occurrence of this fungus led to repeated attempts to secure infection with this organism by reinoculating healthy soil or by placing the fungus directly on roots growing in a special moist chamber. In isolated cases some indication of infection was found, but the negative evidence is so preponderant that it seems highly improbable that Fusarium is the causal organism concerned with the disease in question.

Species of Fusarium are well-known soil saprophytes, and their presence in decaying roots or even on healthy roots is to be expected. This relationship seems to be well demonstrated in a series of isolations made from roots of 7 different crop plants regarded as susceptible to brown root rot and 7 believed to be immune to it. Out of 132 fragments from susceptible roots, 126 yielded Fusarium, and 98 fragments from the immune roots yielded 60 with Fusarium. Since decay was much more common in the susceptible roots, this no doubt accounts for the more common occurrence of Fusarium. Its frequency on apparently immune crops is, however, significant in this connection.

No fungus other than Fusarium could be consistently cultured from diseased roots. A detailed microscopical examination of diseased tissue was therefore resorted to either by means of teasing the tissues apart under the binocular, by means of free-hand razor sections or with stained paraffin sections.

The examination of the roots under the binocular frequently revealed a Rhizoctonialike mycelium in considerable abundance, especially when the roots were torn apart. The strands often appeared to be beneath the cortical tissue, and with needles they could be separated from the host tissue and placed directly on nutrient media in Petri dishes.

The fungus, however, was not readily culturable. In a few instances growth of Rhizoctonia was obtained, but it could not be ascertained that this was the same species or strain which commonly existed on the roots themselves. This strain of Rhizoctonia was culturally somewhat different from the ordinary Rhizoctonia with which we are acquainted. Inoculation experiments, however, again failed to give positive results.

A study of free-hand sections through lesions stained with carbol fuchsin revealed a striking picture in some cases. The cells appeared to be crowded with a very fine mycelium, such as would be expected in the Actinomyces. This lead was followed up carefully for several months. Great difficulty was experienced in isolating this fungus, although apparently it was eventually accomplished. Artificial soil inoculation, however, again failed to yield positive results.

During the course of the investigation various species of bacteria have been isolated. No particular organism, however, has seemed to predominate, and negative results only have been obtained with a number of different species which have been used in inoculation experiments.

Stained paraffin sections were found to be of little value in indicating the presence of a causal organism, although the histological picture of the disease is very well shown. (Figs. 5 and 6.)

EVIDENCE REGARDING THE NATURE OF THE DISEASE

Although it is not believed that the writers have definitely demonstrated that neither Fusarium, Rhizoctonia, Actinomyces, nor bacteria are the cause of brown root rot, the evidence points strongly in that direction. Of the organisms with which they have been concerned, a nonculturable Rhizoctonia would seem most likely to be the parasite involved. There still remains the additional possibility that an unknown parasite is concerned.

Evidence pointing toward the parasitic nature of brown root rot has been repeatedly obtained. This evidence may be summarized as follows:

(1) Soil mixtures: Diseased soil mixed with healthy soil in proportions as low as 10 per cent of the former will result in the production of the disease, although the extent of the disease is roughly proportional to the quantity of diseased soil added.

(2) Diseased roots: If diseased roots are washed free of soil, cut up, and mixed with healthy soil, typical infection can be obtained. Apparently, the roots are proportionally more effective in this respect than diseased soil.

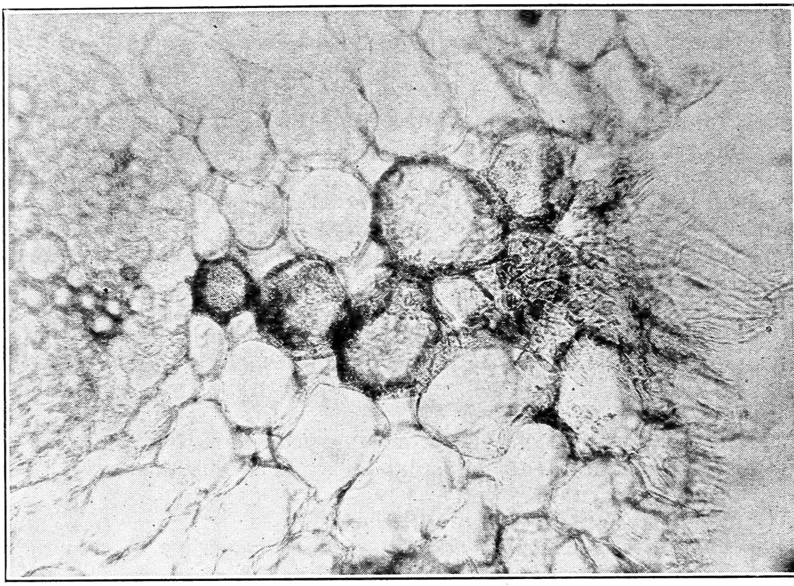

Fig. 5.—Cross section of a root of tobacco showing early stages of brown root rot. The cells usually seem to contain a granular material which, together with the cell walls, is discolored

(3) Steam sterilization: Steam sterilization of the soil effectively destroys the power of diseased soils to produce symptoms of the disease. (Figs. 7 and 8.)

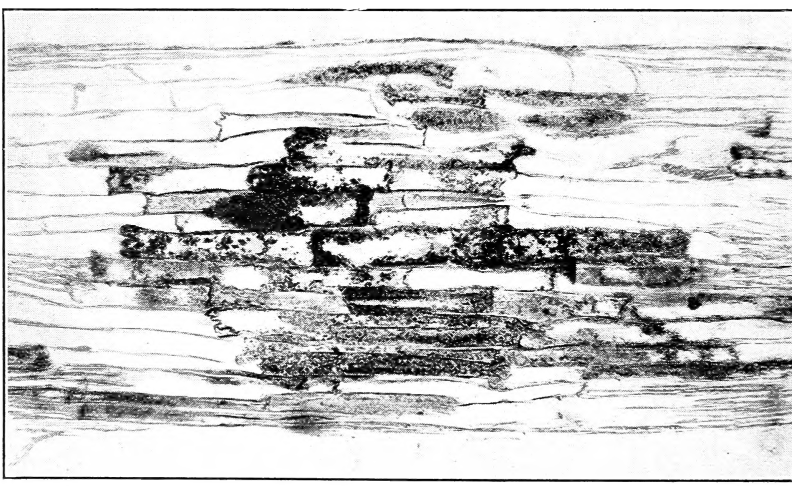

Fig. 6.—A longitudinal section of a root of tobacco affected with brown root rot. Note how sharply the affected cells are delimited from the healthy ones

(4) Formalin sterilization: Treatment of the soil with dilute solutions of formalin (1–50 or 1–100) destroys the ability of the soil to produce symptoms.

(5) Temperature relations: The behavior of the disease on plants grown at different soil temperatures is apparently more closely related to biological than to chemical activity. (Fig. 9.)

(6) Symptoms of disease: The lesions produced on the roots and the response of the plant in general, together with a tendency to recover from the disease under changing environmental conditions, are more or less typical of parasitic root rots.

For several years during the course of this investigation little doubt was entertained that the disease was of a parasitic nature. Ex-

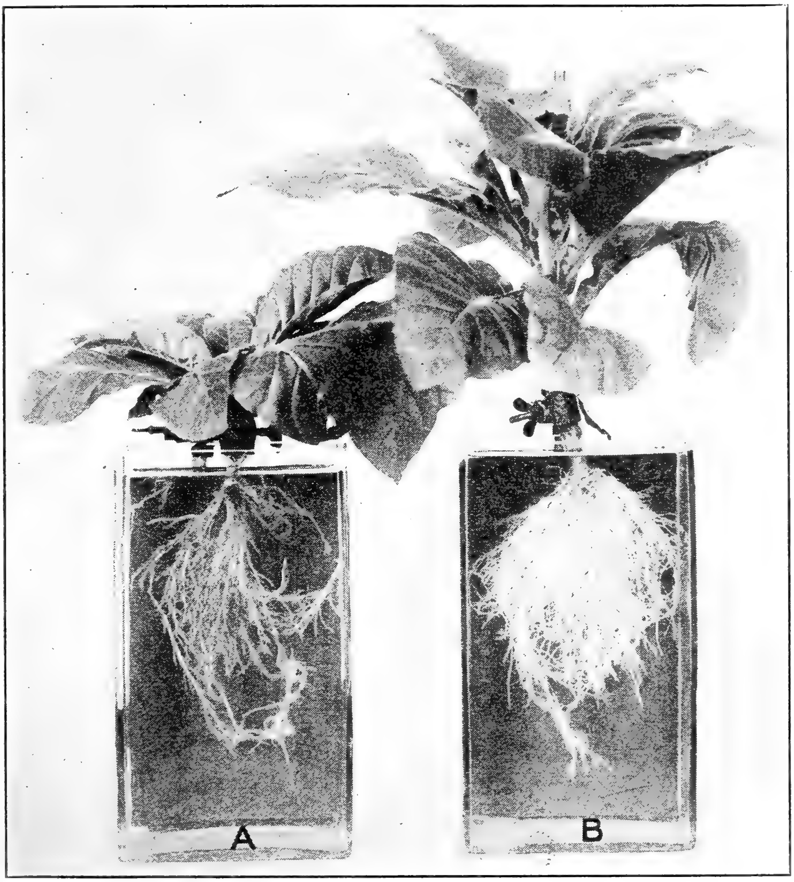

Fig. 7.—Comparison of the growth of tobacco plants: *A*, In soil affected with brown root rot, showing a brown and deficient root system and stunted growth; *B*, in soil like that used for *A* but sterilzed

periments were conducted, moreover, which seemed to indicate that various other factors of a nonparasitic nature were not concerned, such as overfertilization, soil toxins, or soil-air relations.

Two facts have developed, however, during the course of these studies which seem inexplainable on a parasitic basis. Diseased soils spread out in a thin layer and exposed to rapid drying will almost completely lose their power of producing symptoms within as short a time as one to six days. (Fig. 10.) This is true whether in the presence or absence of direct sunlight. This observation seems

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to reduce greatly, if not to eliminate entirely, the common types of plant parasites as causal agencies.

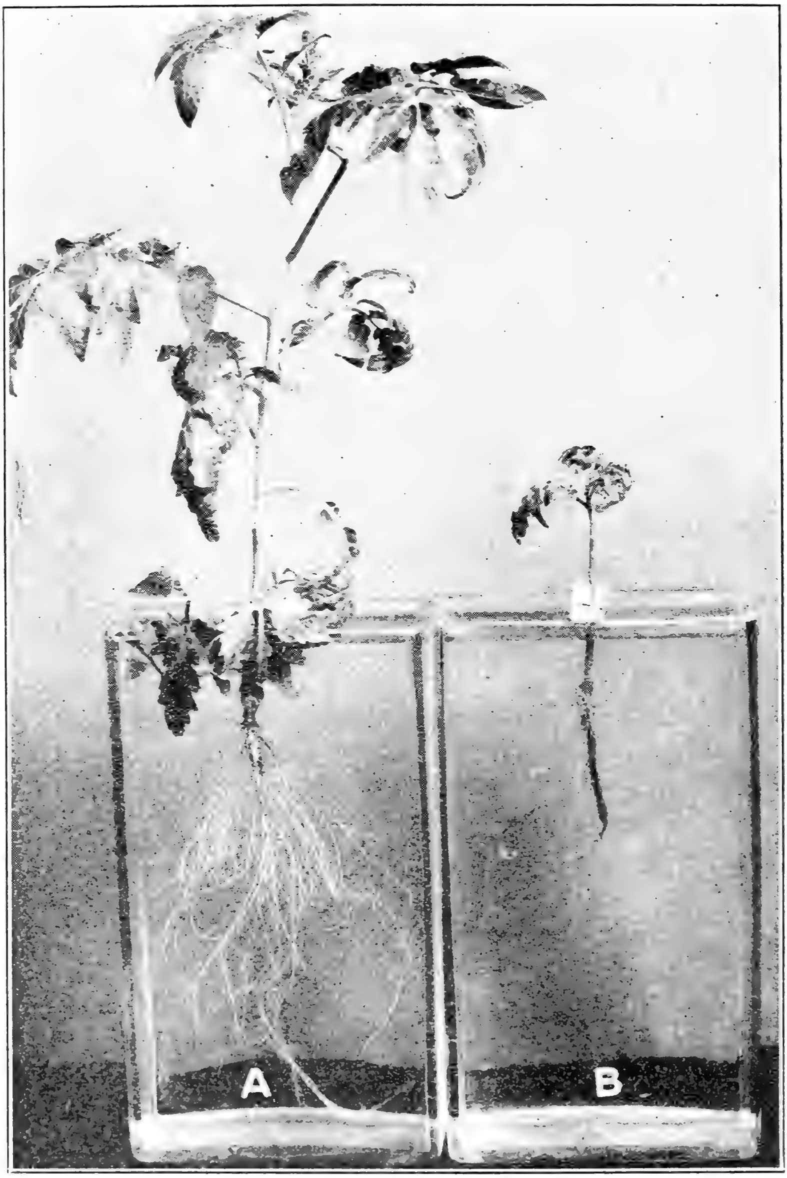

FIG. 8.—Comparison of the growth of tomato plants: *A*, In soil affected with brown root rot, sterilized; *B*, in unsterilized soil of the same kind

Rotation plat experiments indicate, contrary to expectation, that the more common apparently nonhost plants are much more likely to develop or retain the brown root-rot condition in the soil than the typical host plants. The data on this subject will be presented later.

Taking all these results into consideration, the writers have not been able to compare satisfactorily brown root rot with any previously described phenomenon in plants. Whatever the fundamental explanation may be, in a general sense the malady seems to result mainly from the influence of one crop upon another. In this respect it shows considerable resemblance to the injurious action of one plant species upon another when grown in association or when one precedes the other, as described by various workers already referred to who have been concerned with the problem from an agronomic standpoint.

Unfortunately, sufficient details are not given by most of these workers as to the symptoms, if any, exhibited by the roots of the plants which are injuriously affected, to make possible a satisfactory comparison with brown root rot, as described in this bulletin.

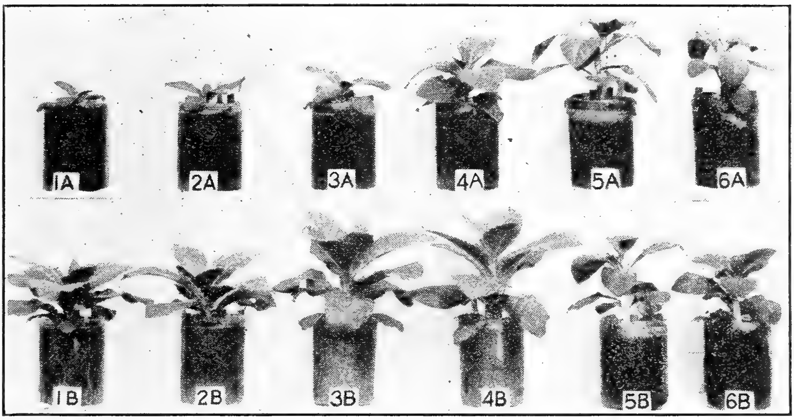

FIG. 9.—Influence of soil temperature on the severity of brown root rot on tobacco plants. Soil affected with brown root rot was placed in the jars of series *A* (above) and the same soil sterilized in series *B* (below). The plants were grown at approximately 18°, 22°, 26°, 30°, 34°, and 36° C., respectively, by immersing the jars in water kept at the stated temperatures

PLANTS AFFECTED

In the absence of a known causal agency the determination of the host range of brown root rot is obviously uncertain. It was deemed important, however, to make some observations along this line, even though conclusions could only be based on gross root symptoms.

Such determinations are much more readily made with some plants than with others. It was found especially difficult to draw satisfactory conclusions on the grasses and grains, since roots on these plants apparently die off readily from natural causes.

Most attention has been given to crop plants which might profitably be grown in rotation with tobacco. In most cases these plants have been grown in brown root rot soil, both in the field and in the greenhouse, with tobacco plants as controls. (Fig. 11.) After growing in the soil for a sufficient length of time to give abundant signs of the disease on tobacco, the plants were removed with the roots, which were washed free from soil and examined for lesions by floating out in water against a white background.

Aside from tobacco, the tomato is probably most vigorously attacked. The symptoms on tomato are much like those on tobacco, and this plant has been frequently used in experimental work in preference to tobacco, for the reason that it is practically immune to Thielavia root rot and consequently is a better index of brown root-rot infection in some soils than the tobacco plant, particularly in soils where the two diseases may be present.

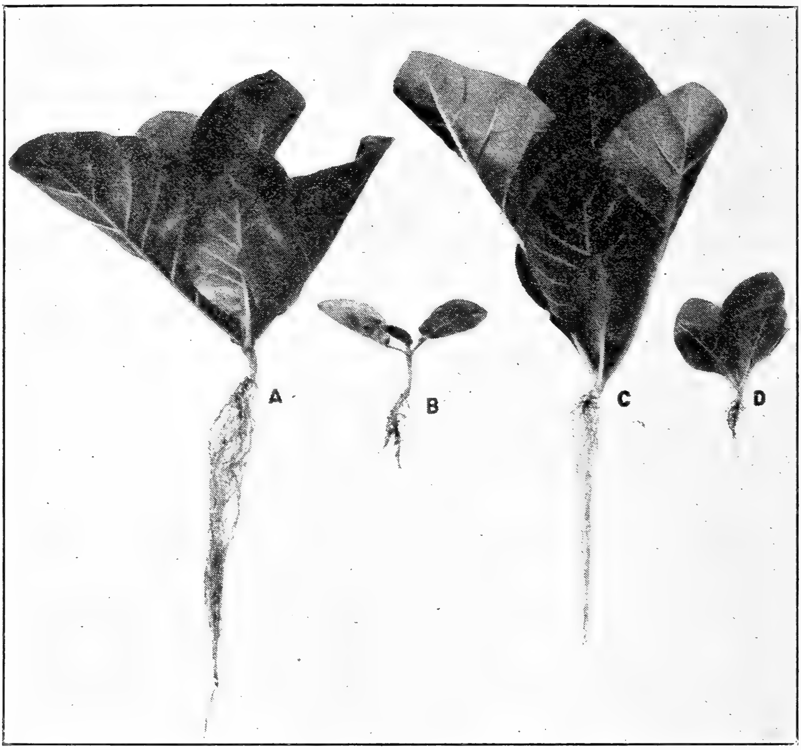

FIG. 10.—Influence of soil drying or aeration on the growth of tobacco plants: *A*, In brown root rot soil dried in a thin layer one week; *B*, in the same soil not dried; *C*, in healthy soil (control); *D*, in healthy soil to which was added a small quantity of washed timothy roots taken from brown root rot soil. Drying or aeration of the soil seems to destroy rapidly the injurious agency which appears to be located, at least in large part, in the organic matter of the soil

The potato, eggplant, and pepper are apparently affected, but much less so than tobacco or tomato, pepper especially being very resistant to it.

Many legumes belong in the susceptible group, although, again, much variation is to be found. Cowpeas, soybeans, garden beans, hairy vetch, and the common clovers belong to the group of moderately susceptible plants.

The common graminaceous crop plants were found difficult to classify, but it may be said with certainty that, so far as evidence of typical root lesions are concerned, oats, barley, wheat, and rye are only very slightly, if at all, affected. Timothy should probably be classified along with these related crops, although one could not readily do so on the basis of the examination of the root system. Only very questionable root lesions have been found on corn.

Cabbage, onions, beets, pumpkins, cucumbers, and lettuce apparently are practically, if not entirely, resistant to any injurious action from brown root-rot soil.

There is room for considerably more experimental evidence along the line of host range, but the work was discontinued largely because of the fact that this information was not leading to any important conclusion relative to either the cause or control of brown root rot; that is, it has not been evident from subsequent experimental work that the occurrence of root lesions bore any direct relation to the increase or overwintering of the disease in the soil. It can not yet be concluded that the disease has its origin with any particular natural or cultivated vegetation, although, as shown later, it is apparently accentuated by some crops more than by others.

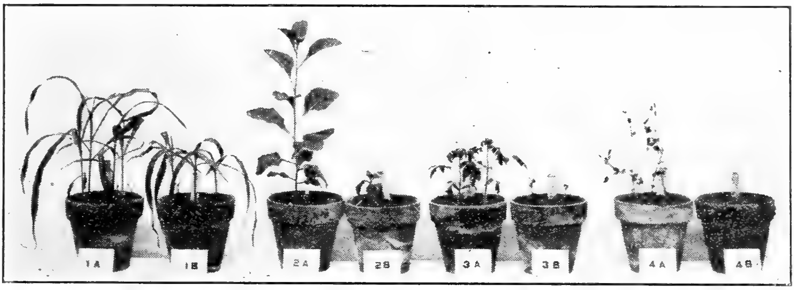

FIG. 11.—Growth of corn (1), tobacco (2), tomatoes (3), and peas (4) in steam-sterilized (*A*) and unsterilized (*B*) brown root-rot soil. These soils are sometimes extremely detrimental to the growth of various crops, although the injurious agent is not definitely known to be the same on all hosts. Steam sterilization has also some beneficial effect on soil productiveness

Brown root rot, however, appears to be associated with the character of the soil itself as well as with its distant cropping history.

VARIETY AND STRAIN TESTS WITH TOBACCO

In the case of black root rot of tobacco it has been shown that very decided differences in resistance to disease occur (*10*). Eight of the more typically resistant and susceptible strains were planted on a brown root rot field at Whately, Mass., in 1918. The results were negative to a striking degree. (Fig. 12.) Apparently, the Thielavia-resistant varieties succumbed as readily as the other varieties to the brown root rot. Similar though less striking results were secured on other plats in the same year, and where difference in resistance occurred it was found to be attributable to soil infested with Thielavia (black root rot).

Brown root-rot fields, however, often show an unevenness of growth suggesting individual differences in the resistance of plants. (Fig. 13.) Several of these outstanding plants were selected from "sick" soils and the seed planted the following year in progeny rows, but the results were at once discouraging. The writers are strongly inclined to believe, therefore, that no appreciable variation in resistance to brown root rot occurs in varieties of tobacco (*Nicotiana* *tabacum).* Whether or not different species of tobacco will respond differently has not been determined.

INFLUENCE OF SOIL CONDITIONS

The writers have naturally been led to make some observations and to conduct certain experiments bearing on the relation of the environment and other conditions in the soil to the occurrence and severity of brown root rot. It has already been pointed out that experimentally this disease is apparently very sensitive to desiccation or aeration, acting jointly or separately. How far these factors influence the disease in the field has not been satisfactorily determined. It is likely, however, that the prevalence of the disease may be materially influenced by the cultivation practices under certain weather conditions, and this line of experimentation may prove profitable. One is naturally led to consider the rôle played by this factor in explaining the striking influence of the rotation system on the disease.

FIG. 12.—Influence of brown root-rot soil on the growth of varieties of tobacco, showing eight varieties markedly different in resistance to Thielavia root rot. These are all about equally affected in this diseased soil. Little, if any, varietal difference in resistance to brown root rot appears to exist

Though the writers have not conducted any experiments on the relation of the physical condition of the soil to the disease, it seems very evident that no close correlation exists. The disease frequently occurs in spots in the field, but it does not seem to bear any consistent relationship to topography. The condition occurs in coarse sandy soils as well as in soils with a considerable percentage of silt or clay. In the absence of a known causal agency, however, it is not yet possible to say that the brown root rot found in the typical tobacco soils of Kentucky and Wisconsin is identical with that occurring in the Connecticut Valley.

By means of screening and floating out the organic matter from the soil, the writers were able to show that a large part of the injurious agent of brown root rot exists in the organic matter; further than this, no evidence was found as to its relation to the disease. It may be said, however, that the disease appears to exist in soils relatively very low in organic matter.

In greenhouse and in field experiments, the application of commercial fertilizers to brown root-rot soils has frequently resulted in marked increases in yield, but these apparently contradictory results may be explained on the basis of environmental conditions. They are significant only in that they seem definitely to overthrow the hypothesis sometimes suggested that brown root rot is a consequence of over-fertilization of the soil. In a practical sense, however, it is to be regarded as poor practice to attempt to bring about good yields in brown root-rot fields by the application of fertilizers. This conclusion may be illustrated by the results obtained on the heavily fertilized experimental plats at Whately, Mass., in 1922, where the yield of tobacco ran as low as 460 pounds per acre as compared with a yield of more than 100 bushels of corn. (See Table 2, p. 21.)

FIG. 13.—A field of tobacco at Whately, Mass., badly affected with brown root rot. The bagged plant was selected for resistance to disease, but later this plant, along with others, proved to be of no value

The tobacco soils of the Connecticut Valley are on the whole more or less acid in reaction. A considerable number of determinations have been made in connection with this work, both by the Truog method and the colorimetric method for H-ions. These determinations have been made largely on diseased soils, but normal soils have been used for comparison. The conclusion is justified from these results that the acid reaction of the soil bears little, if any, relation to brown root rot. In experiments planned to determine the influence of liming soils on the growth of tobacco, there is some indication that lime is slightly detrimental rather than beneficial on brown root-rot soil, although lime may be somewhat beneficial to soils free from disease.

It has been shown that soil temperature has a very decided influence upon the severity of the black root-rot disease of tobacco (*13*). Experiments of a similar nature were made with brown root-rot soil taken from typically diseased soils in the Connecticut Valley (fig. 9). The experiments along this line have not been extensive, but it seems apparent that the optimum temperature for the development of brown root rot lies between 20° and 26° C., and that above 27° the number and extent of the lesions are much reduced, very few, if any, occurring above 31° C. Everything considered, brown root rot is favored by higher temperatures than black root rot, and it is doubtful whether sufficiently high soil temperatures to inhibit the disease materially in the field ever occur in the Connecticut Valley.

Two series of experiments conducted with varying degrees of moisture in brown root-rot soil were not convincing, but indicated that a fairly constant percentage of soil moisture within limits for normal plant growth did not markedly influence the extent of the damage from the disease. Dry weather apparently increases the injurious action of root rot under field conditions, however, since the ratio between functioning roots and the soil moisture may be greatly reduced within a comparatively short time.

On the other hand, new roots comparatively free from disease may develop in relatively dry soil and will function for some time following rains and permit a partial and often a very marked recovery of growth, which is not evident in diseased soils remaining continually moist during seasons of excessive rainfall.

INFLUENCE OF DRYING AND AERATION

Small quantities of soil have been shipped for several years from a number of different brown root-rot fields in the Connecticut Valley to the Wisconsin laboratories. Frequently portions of these soils not used during the winter months immediately following for greenhouse experiments were used the subsequent fall, or one year after having been taken from the field and stored under cover, where they gradually dried out. These stored soils generally seemed to have lost all or a greater part of the ability to produce brown root rot.

Experiments were consequently undertaken with two different brown root-rot soils, one being from the Helen Crafts farm, Whately, Mass., where rotation experiments were conducted, the other soil of a very sandy type on which a crop failure due to brown root rot occurred the previous season.

Various methods of drying were resorted to, and the results of different experiments naturally varied with the rate of drying or aeration, depending upon the thickness of the layer of soil used and the atmospheric conditions prevailing. Early experiments showed that soil spread in a relatively thin layer and allowed to dry for two weeks with occasional stirring showed a remarkable decrease in brown root rot, as measured by plant growth and the number of lesions on the roots. This effect was somewhat more marked in the sandy soil than in the heavier soil, which had greater water-holding capacity. The increase in growth was estimated to be as much as 1,000 per cent in the sandy soil one month after planting.

The experiment was now varied to compare drying in the absence of direct sunlight and in direct sunlight. To exclude direct sunlight the soil was covered with paper in one case and placed in a dark room with a current of air passing over the soil in the other case. The soils when dried for one week, whether exposed to sunlight or not, produced a growth of tobacco approximately six times as great as the untreated controls. Similar experiments were repeated several times with like results, except for the fact that the period of drying could be shortened to one to two days with almost as good results, provided the layer of soil was made sufficiently thin and a good current of air passed over it. It was very evident that sunlight was not the effective agent.

It is reasonable to assume, however, that aeration of the soil rather than desiccation may have been the active agent in destroying brown root rot in these experiments. Attempts at aerating the soil without drying by drawing the air through cylinders of the soil gave negative results, but it is not likely that all parts of the soil are uniformly exposed under these conditions.

Aeration of the soil by spreading it in a thin layer before an electric fan, keeping it moist by watering two or three times daily, was then tried. Parts of the soil, however, did dry for short periods. Tests by growing plants in this soil showed that the aerated moist soil gave equally as good control of the disease as the aerated dry soil. This experiment when repeated with two soils, aerating dry and moist for one week, gave an improvement of as much as 600 per cent with moist aeration, but dry aeration was apparently still more effective. Further experiments gave conflicting results as to the relation of aeration in the presence and absence of moisture. A more satisfactory method for conducting such studies should be developed, since it was found difficult to repeat the experiments in such a way as to make certain that similar treatments were given in all cases.

The writers are therefore not prepared to state definitely, whether desiccation or aeration, or both, were most concerned in the destruction of brown root rot in these experiments, although they are inclined to believe from their preliminary experiments that both play a part.

FIELD-PLAT EXPERIMENTS

It was recognized before the laboratory work on brown root rot progressed very far that it was important to obtain more reliable information upon the relation of different crops to the disease under field conditions, with the hope that a system of rotation might be found which would aid in remedying the trouble. On account of unforeseen difficulties, however, a satisfactory start in rotation experiments was not obtained until 1922.

A series of plat experiments was conducted on the farm of Spenser Bros., Suffield, Conn., in 1919, on land which gave practically a crop failure the preceding year, due apparently to brown root rot. The outstanding results from these plats were that the greenhouse tests on crops affected were essentially corroborated. The excellence of growth of such crops as potatoes and corn, compared with relatively poor yields of tobacco, was indicative of the general productiveness of the land following fertilizer treatment. On the other hand, this soil was much improved for tobacco by the liberal application of fertilizer, so that no sharp line of distinction can be drawn between failure due to brown root rot and that due to lack of fertility.

Liming the soil in combination with the fertilizer treatment apparently increased the injury, but the application of sulphuric acid had little effect. Formalin sterilization of the soil resulted in the production of roots free from disease. In this case the beneficial action was probably due largely to the formalin rather than to the effects of desiccation or aeration, as might be the case in the laboratory experiments where the soil was spread out to dry after treatment.

In 1920, fertilizer plat experiments were placed on the farm of W. A. Haviland, at East Windsor Hill, Conn. The nature of the trouble on this land was not definitely known, except that it was regarded as "tobacco sick." Various combinations of fertilizers were applied, and varieties differing in resistance to black root rot were grown. Nitrogen was found to be the controlling fertilizer element, and smaller increases were obtained with phosphorus and potassium. Thielavia root rot was so abundant, however, that any results bearing on brown root rot were obscured. It is interesting to note, however, that lime again retarded growth and maturity on these plats.

In 1921, preliminary arrangements were made to conduct rotation experiments on the farm of Helen Crafts at Whately, Mass., on a soil which was affected with typical brown root rot. Land was also selected for a similar set of plats at the tobacco substation of the Connecticut Agricultural Experiment Station at Windsor. The latter land was not affected with brown root rot, but the expectations were that it would develop during the course of the experiments. The experiments on these soils were started in 1922 and continued through 1923 and 1924, forming the basis of the present report.

PLAN OF THE EXPERIMENTAL PLATS

The experiments were planned primarily to determine the influence of rotating crops, both susceptible and immune to brown root rot, with tobacco. Other plats were added, however, to determine the influence of fallowing, liming, and heavy fertilizer application.

Included in each experiment were 22 twentieth-acre plats. Corn, onions, and timothy were selected to represent crops not attacked by brown root rot, and tobacco, tomatoes, potatoes, beans, and clover represented crops more or less definitely affected. The selection was to some extent influenced by the agricultural crops commonly grown in the community. In the original plan these crops were to be grown on their respective plats two years, followed by tobacco on all plats the third year. In 1923 it was decided, however, to divide the Whately plats into halves and to plant one of each to tobacco, in order to determine the influence of one season of the respective crops on the growth of tobacco. In 1924 all plats were planted to tobacco, so that the effect of two years' growth of the various crops was obtained, as well as the residual effect of one year's cropping in comparison with tobacco in continuous culture.

The duplication of plats was begun in the opposite corners of the experimental area, so as to compensate as much as possible for the natural variation in the land.

The general plan of the plats is best understood by referring to Table 1.

TABLE 1.—*Succession of crops and fertilizer applications on the brown root-rot plats at Whately, Mass.*

Plat	Crop grown				
	1922: A and B series	1923		1924	
		A series	B series	A series	B series
No. 1	Corn	Corn	Tobacco	Tobacco	Tobacco.
No. 2	Timothy	Timothy	do	do	Do.
No. 3	Beans	Beans	do	do	Do.
No. 4	Potatoes	Potatoes	do	do	Do.
No. 5	Tomatoes	Tomatoes	do	do	Do.
No. 6	Fallow	Fallow	do	do	Do.
No. 7	Onions	Onions	do	do	Do.
No. 8	Tobacco	Tobacco	do	do	Do.
No. 9 (double fertilizer application)	do	do	do	do	Do.
No. 10	Clover	Clover	do	do	Do.
No. 11 (limed)	Tobacco	Tobacco	do	do	Do.
No. 12	Corn	Corn	do	do	Do.
No. 13	Timothy	Timothy	do	do	Do.
No. 14	Beans	Beans	do	do	Do.
No. 15	Potatoes	Potatoes	do	do	Do.
No. 16	Tomatoes	Tomatoes	do	do	Do.
No. 17	Fallow	Fallow	do	do	Do.
No. 18	Onions	Onions	do	do	Do.
No. 19	Tobacco	Tobacco	do	do	Do.
No. 20(double fertilizer application)	do	do	do	do	Do.
No. 21	Clover	Clover	do	do	Do.
No. 22 (limed)	Tobacco	Tobacco	do	do	Do.

TESTS AT WHATELY, MASS.

The Whately plats were located on a level medium-sandy loam soil. The field had been in timothy following failures with tobacco in 1917 and 1918. This field was used by the senior writer in 1918 in connection with studies on varietal resistance tests, and the stunting of all varieties on this land indicated that it was not only a typical brown root-rot soil but also that Thielavia root rot was not present to any extent.

The timothy sod was plowed on April 25, and following a thorough preparation of the land twentieth-acre plats were laid out. An application of 175 pounds of approximately a 6–5–6 commercial fertilizer was made to each plat, plats 9 and 20, however, receiving a double application and plats 11 and 22 being treated with 100 pounds of lime in addition. The crops were planted in their respective seasons, except that the onions were planted somewhat too late for the best results.

Good crops of corn, timothy, and clover developed, reaching average heights of more than 12 feet, 18 inches, and 12 inches, respectively. The beans, potatoes, tomatoes, onions, and tobacco, however, made only slow progress, apparently for different reasons. In the case of tobacco and tomatoes the main injurious agent was apparently brown root rot, but other diseases probably influenced the results with beans and potatoes. Data on the weight of beans were not obtained, since they did not mature, but the vines reached a height of 1 foot. The onions also grew to a height of 1 foot but produced only scallions, so that the yield was not recorded. The data for the other crops are shown in Table 2. It will be seen that the 1922 yield of tobacco was very poor, as compared with the yield of corn (fig. 14). Double fertilization, that is, 7,000 pounds of 6–5–6 fertilizer per acre gave a considerable increase in yield over a single application, and liming was apparently injurious to growth.

In 1923 the plats were divided in such a manner that tobacco followed each of the other crops used in the rotation on one half of each plat, the other half being grown to the same crop as in 1922. It was found necessary to reseed the clover on plat 10–A, apparently as a consequence of damage by rodents the preceding season.

Fertilizers were again applied to all plats at the rate of 4,000 pounds to the acre of a 6–5–6 mixture, except plats 9 and 20, which received fertilizer at the rate of 8,000 pounds per acre. Plats 11 and 22 were again treated with lime at the rate of 2,000 pounds per acre.

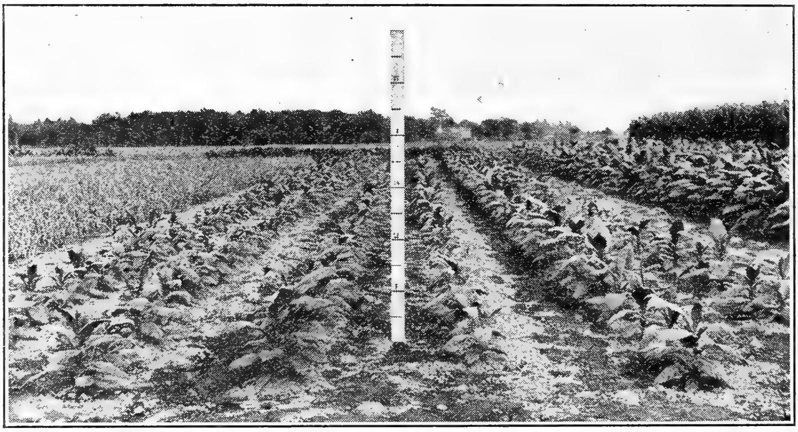

FIG. 14.—Part of experimental plats at Whately, Mass., in 1922. Onions are shown to the extreme left, the failure of the tobacco crop on plat 8 is shown in the center, whereas an excellent corn crop may be seen at the extreme right

A good stand of all crops was secured, although rodents damaged the beans to such an extent that data on yield could not be obtained. The effect of the preceding year's cropping on the growth of tobacco was very striking during the entire growing season and contrary to expectations or the assumption of a parasitic hypothesis for brown root rot, although not out of line with certain observations made in former years. The growth of tobacco after timothy and corn (figs. 15 and 16) was extremely poor, the crop being practically worthless. On the other hand, the growth following tobacco and the fallowing (figs. 17 and 18) of the land was very good in comparison, the growth following the other crops grading between these extremes. The final yields of the rotation crops in 1923 are shown in comparison with the 1922 results in Table 2. It may be noted that the average yield from the single fertilization exceeds that of the double fertilization and that the lime plat is intermediate in this respect in

1923. The differences are, however, too small to be significant. It is interesting to compare the estimated market value of the crops from the various plats on the basis of yield and quality. On the basis of 12 cents per pound for the poorest grades and 40 cents for the best grade of tobacco, the value of the crop following timothy was computed to be $52.80 per acre, whereas that from the single-fertilized tobacco plat was $624 per acre.

Table 2.—*Yields of crops on brown root-rot rotation plats located at Whately, Mass., showing the influence of various crops on the succeeding yield of tobacco*

[Acre yields in pounds except as otherwise stated]

Crop in rotation	Plat	Yields of crops in rotation		Yields of cured tobacco (pounds)		
		1922; A and B series	1923; A series	1923; B series	1924 A series	1924 B series
Corn (yields in bushels)	No. 1	112	108	680	400	1,060
	No. 12	107	100	400	280	1,040
Average		109.5	104	540	340	1,100
Timothy (yields in tons)	No. 2	3.15	4.0	480	320	1,240
	No. 13	2.2	3.1	400	240	920
Average		2.67	3.55	440	280	1,080
Beans	No. 3			1,040	1,120	1,600
	No. 14			800	960	1,160
Average				920	1,040	1,380
Potatoes (yields in bushels)	No. 4	140	229	1,160	1,200	1,520
	No. 15	96	247	1,000	1,240	1,440
Average		118	238	1,080	1,220	1,480
Tomatoes (yields in tons in 1922, in bushels in 1923)	No. 5	3.5	300	1,360	1,320	1,640
	No. 16	2.1	280	1,400	1,240	1,520
Average		2.8	290	1,380	1,280	1,580
Fallow	No. 6			1,480	1,640	1,640
	No. 17			1,440	1,640	1,480
Average				1,460	1,640	1,560
Onions (yields in bushels)	No. 7		428	1,440	1,320	1,440
	No. 18		160	1,120	1,360	1,400
Average			294	1,280	1,340	1,420
Tobacco	No. 8	460	1,600	1,600	1,600	1,600
	No. 19	600	1,520	1,520	1,740	1,740
Average		530	1,560	1,560	1,670	1,670
Tobacco (double fertilization)	No. 9	540	1,520	1,520	1,520	1,520
	No. 20	780	1,480	1,480	1,600	1,600
Average		660	1,500	1,500	1,560	1,560
Clover (yields in tons)	No. 10	2.7		480	320	880
	No. 21	1.0	2.0	720	640	1,080
Average		1.85		600	480	980
Tobacco (limed)	No. 11	380	1,460	1,460	1,340	1,340
	No. 22	740	1,560	1,560	1,500	1,500
Average		560	1,510	1,510	1,420	1,420

In the 1924 season all plats were fertilized as in 1923 and planted to tobacco. In the crop-succession plats, tobacco consequently fol-

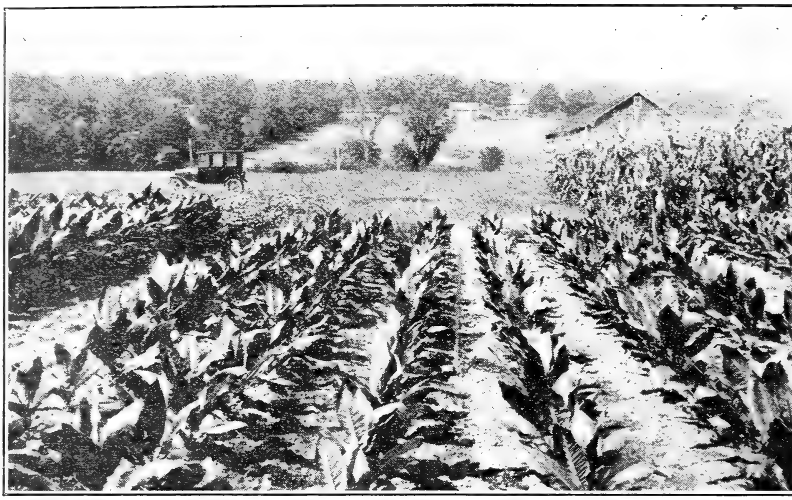

FIG. 15.—Tobacco growing after timothy on plat 2–B at Whately, Mass., August 24, 1923

lowed two years of the respective crops on one half of each plat, which in turn were preceded by several years of timothy sod. The other half plat may be considered to be a measure of the residual

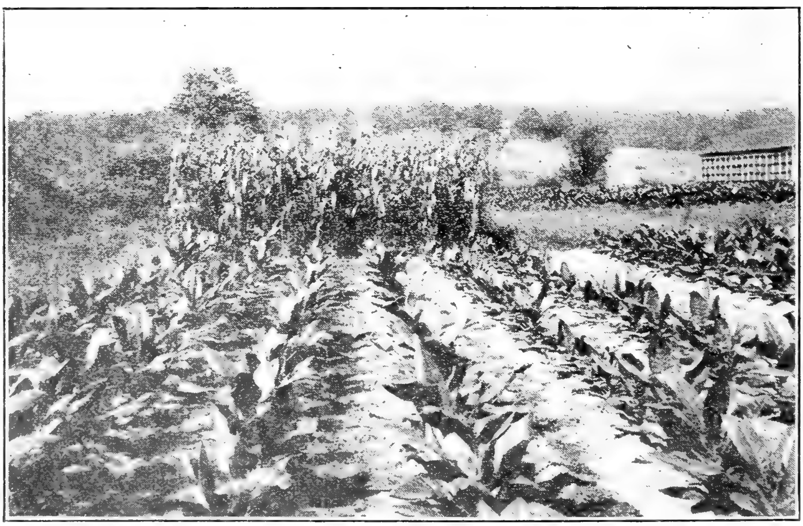

FIG. 16.—Tobacco growing after corn on plat 12–B at Whately, Mass., August 24, 1923; plat 12–A, planted to corn, in the background

effect from one year's cropping to the respective crops, or as an indication of the rate of recovery from brown root rot following cropping to tobacco for one season.

The results were even more striking in 1924 than in the preceding year, following, however, the same general trend. (Figs. 19 and 20.) The tobacco crop was poorest after timothy, followed closely by tobacco after corn and after clover. The best yields followed tobacco and fallow. Yields after onions, tomatoes, potatoes, and beans occupied an intermediate position. Comparing the relative yields with those of 1923 (Table 2) it seems apparent that the injurious action following timothy, corn, and clover is increased by two years of these crops as compared with one year's cropping. The single-fertilized plats are again somewhat better than the double-fertilized plats, and a fairly marked falling off in yield on the lime plat may be noted.

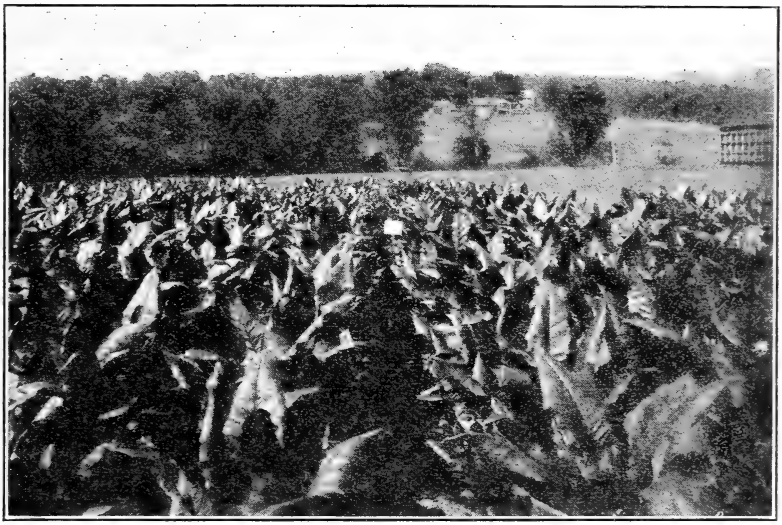

FIG. 17.—Tobacco growing after tobacco on plat 8 at Whately, Mass., August 24, 1923. Compare with Figure 16

By comparing the yields in the B series of plats, namely, those following a crop of tobacco in 1923, preceded, in turn, by the respective crops used in rotation, a remarkable recovery from the brown root-rot condition, as indicated by increased yields, is evident in the timothy, corn, and clover plats and to a lesser extent following beans, potatoes, tomatoes, and onions, whereas in the plats growing the third crop of tobacco there is no significant increase over that of the preceding year. On the other hand, if we compare the yields in the B series in 1924 with each other it is evident that there is still a residual effect of the crop grown two years previously, this effect being much more marked in the case of timothy, corn, and clover than with the other crops. The yields of tobacco in continuous culture and the fallow plats during 1922, 1923, and 1924, indicate that no residual effect from the injurious action of timothy of 1921 and preceding years existed in 1924. In other words, judging by these experiments, the injurious agent apparently disappears when the crops which act injuriously are kept off the ground for two years.

TESTS AT WINDSOR, CONN.

The plats located at Windsor, Conn., were essentially a duplication of those at Whately, so far as the plan of the experiments and treatment are concerned. The soil was known not to be affected with brown root rot. It was believed, however, that it might develop the disease under one or the other system of cropping; but this did not prove to be the case. The soil in the plats at Windsor varied from a light sand to a light sandy loam. Unfortunately, part of plats 18 to 22 lay in a corner of the field affected with black root rot, and consequently the yield of tobacco from these plats is probably not so high as it otherwise would have been. This, together with other soil variations, probably accounts for the differences in yield of duplicate plats placed on opposite sides of the

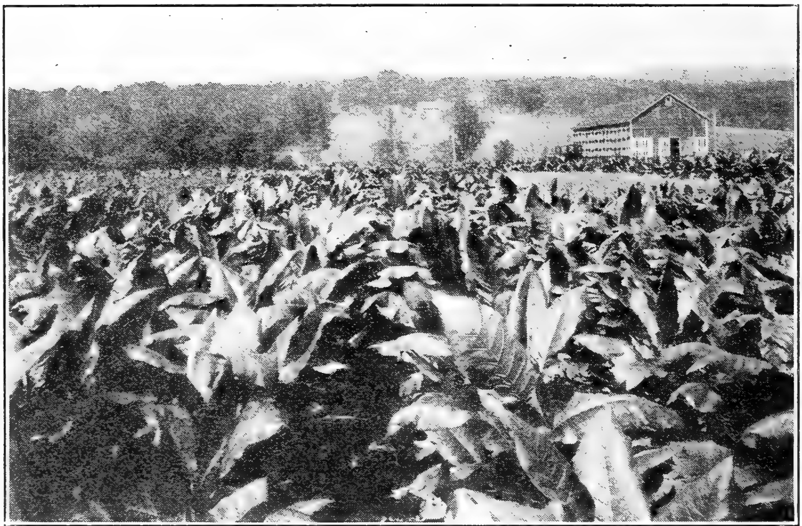

FIG. 18.—Tobacco growing after fallow on plat 17–B at Whately, Mass., August 24, 1923. Compare with Figure 15

experimental area. The land had been seeded to timothy several years prior to 1922.

There seems to be no good reason for discussing in detail the results of the three years in which these plats were conducted, so far as brown root rot is concerned. They served the useful purpose in this connection of acting as a control upon the Whately plats. The yields on these plats are presented in Table 3, which adequately serves to show that on this particular land and in the absence of brown root rot, timothy, corn, or clover had no such injurious action on subsequent crops of tobacco as was shown in the Whately plats. This statement is, of course, superfluous in the light of practical experience and other experimental data; yet it should be made clear that it is only on certain soils or under certain conditions that brown root rot occurs and that the cropping system probably bears a contributing rather than a causal relationship.

TABLE 3.—*Yields of crops on rotation plats located at Windsor, Conn., where brown root rot did not develop as a factor in crop production*

[Acre yields in pounds except as otherwise stated]

Crop in rotation	Plat	Yields of crop in rotation		Yields of cured tobacco (pounds), 1924
		1922	1923	
Corn (yields in bushels)	No. 1	80	44	763
	No. 11	132	77	1,000
Average		106	60.5	881.5
Timothy	No. 2	600	2,000	900
	No. 12	1,600	3,500	1,125
Average		1,100	2,750	1,012.5
Beans (yields in bushels, shelled)	No. 3	29	28	825
	No. 13	30	25	1,075
Average		29.5	26.5	950
Potatoes (yields in bushels)	No. 4	323	237	838
	No. 14	355	197	1,050
Average		339	217	944
Tomatoes (yields in tons)	No. 5	11.6	22.8	925
	No. 15	16.5	20.4	1,125
Average		14.1	21.6	1,025
Fallow	No. 6			925
	No. 16			1,025
Average				975
Onions (yields in bushels)	No. 7	120	64	1,050
	No. 17	160	78	1,038
Average		140	71	1,044
Tobacco	No. 8	480	1,400	1,138
	No. 18	500	1,440	1,000
Average		490	1,420	1,069
Tobacco (double fertilization)	No. 9	740	1,440	1,213
	No. 19	730	1,420	1,000
Average		735	1,430	1,106.5
Clover	No. 10	2,200	3,800	1,150
	No. 20	1,800	4,000	975
Average		2,000	3,900	1,062.5
Tobacco (limed)	No. 21	720	1,400	1,100
	No. 22	700	1,400	1,037
Average		710	1,400	1,068.5

DISCUSSION OF RESULTS

The outstanding features of the brown root-rot problem have been the failure to ascribe it to any definite causal agency and the striking effect of the crop-rotation system upon the occurrence of the malady.

The problem as to whether brown root rot is of parasitic or nonparasitic origin remains unsettled. The evidence pointing toward the parasitic nature of the disease would be very convincing in the absence of certain observations to the contrary. Though the writers have not studied the literature carefully, there seems to be no fungus or bacterium known to behave like the causal agency as regards exposure to desiccation or aeration in the absence of sunlight. On the other hand, this behavior is not in all cases typical of toxic soil constituents which may have arisen from the decomposition or disintegration of organic or mineral matter. Toxins to be harmful must be appreciably soluble and attain a toxic concentration. These experiments indicate that the causal agency in brown root rot apparently is not soluble in water and furthermore that it is not destroyed, although greatly reduced in activity, by dilution. The behavior in these diluted soils is more like that which might be expected in diluting organisms, except that, so far as the writers have been able to observe, no apparent marked increase of the injurious agent follows when affected plants are repeatedly grown in the diluted soil. It is believed, however, that the logical mode of attacking the problem would now be from a chemical point of view, with the idea of determining more definitely than the writers have

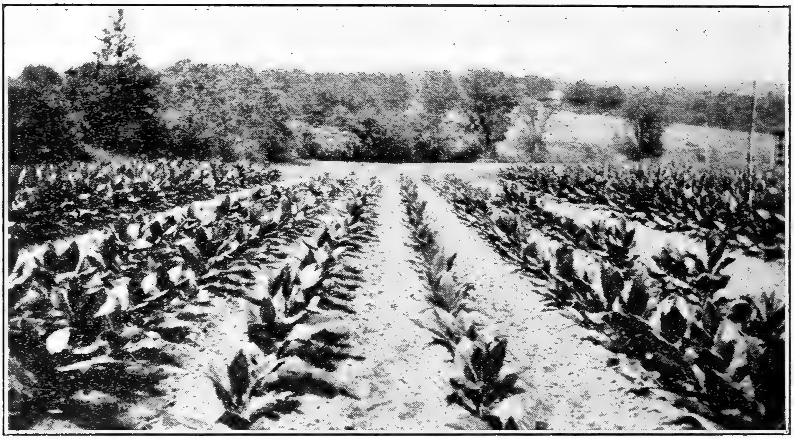

Fig. 19.—Tobacco growing after clover on plat 10–A at Whately, Mass., August 15, 1924

been able to do the relationship between brown root rot and some of the soil phenomena of a more or less obscure chemical origin.

The behavior of brown root rot in the cropping experiments at Whately, although contradictory to a parasitic explanation of the disease, does not necessarily eliminate it. The writers are inclined to believe that the disappearance of brown root rot from the soil when grown to tobacco and certain other crops is in some way related to its disappearance when the soil is dried and aerated. There is some practical basis for this hypothesis also when the relative extent of summer cultivation received by the various crops is considered. That tobacco, tomato, and similar crops destroy the injurious agent by oxidation or by other means seems disproved by the fact that fallow plats recover equally well.

The development of the brown root rot is just as remarkable as its disappearance. Such crops as timothy, corn, and clover are apparently excellent examples of agencies either producing or contributing to the cause. There seems to be no evidence, however, that the causal agent is particularly injurious to the growth and normal development of these crops. Although root lesions apparently occur on clover, the writers can find no evidence that such is the case on corn. That these crops do not produce the injurious action in all soils is evident from their behavior on other soils.

The relation between the problem described in this bulletin as brown root rot and that described by various authors (*1*, *5*, *6*) as crop effects remains to be ascertained. From present indications these may or may not be separate problems. The senior writer has frequently noted cases of the injurious effect of sod on tobacco where brown root-rot symptoms were not present to a sufficient extent to account for the reduced yield. Where brown root rot does occur it seems logical to attribute all or part of the reduced yield to the decay of the root system, although it is conceivable that this may not always be the case. Until more is known, however, about the production of toxic substances in the soil and their action

FIG. 20.—Tobacco growing after tobacco on plat 9 at Whately, Mass., August 15, 1924. Compare with Figure 19

on plants it will be difficult to distinguish between cause and effect in their relation to plant growth.

The results from the crop-rotation plats at Whately are believed to be applicable to a large number of soils in the Connecticut Valley; that is, the disease, which has been studied and observed in a large number of different soils, is believed to be due to the same cause and consequently would respond similarly to the same treatment. The results should therefore have an important practical bearing on the control of the trouble. The logical system of crop rotation, from the standpoint of general agriculture, is not apparently a desirable one on soils likely to be affected with brown root rot, so far as tobacco, tomatoes, and certain other crops are concerned. Continuous culture is probably much more desirable on these soils. This system will naturally lead to other difficulties, but according to present indications, these can more readily be controlled than brown root rot. The most serious objection to the continuous culture of tobacco on the same land is the frequent occurrence of Thielavia root rot. The possibility of controlling this disease by the development of disease-resistant strains is, however, very promising.

SUMMARY

Brown root rot is a name used to designate a condition on the roots of tobacco and other plants which is characterized by a brown discoloration and decay of the root system, resulting in a stunting of the affected plants.

This disease is especially common in the tobacco soils of the Connecticut Valley, where it causes large losses to the tobacco industry. Brown root rot also apparently occurs to a serious extent in other tobacco-growing districts, but it has not been established that the causal agency is the same in all cases.

In many respects brown root rot has the appearance of a disease due to a parasitic organism. Its behavior with respect to soil sterilization, infection, dilution of soil, and relation to environmental conditions indicates a parasitic origin. No causal organism, however, has been demonstrated to be definitely associated with the disease.

The behavior of brown root-rot soils when exposed to desiccation and aeration is not favorable to a parasitic hypothesis. The results of crop-rotation experiments as well as the information gained from a survey of the disease in the field indicate a crop relationship which is contradictory to an explanation based on parasitism. A nonparasitic or chemical explanation of the disease, however, has not yet been found, and the actual nature of the causal agency therefore remains unsolved.

In addition to tobacco, several other crop plants may be affected, notably tomatoes, potatoes, and certain legumes. No lesions are apparent on such crops as corn, onions, cabbage, and beets. Whether timothy and cereals are attacked was not satisfactorily determined.

In a crop-rotation system with tobacco, certain of the crops apparently not affected at all or not seriously affected by brown root rot favor the development or persistence of the disease in the soil, whereas the commonly affected plants, like tobacco and tomato, seem to favor the disappearance of the disease from the soil.

Whatever scientific explanation of brown root rot may eventually be developed, the observations of the disease over a period of years and the experimental results reported in this bulletin point toward a possible means of control by attention to the rotation or cropping system practiced. Final conclusions as to the best practices in this respect need further verification, however, before they can be generally recommended.

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