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CONSIDERATIONS AND EXPERIMENTS ON THE SUPPOSED INFECTION OF THE POTATO CROP WITH THE BLIGHT FUNGUS (*PHYTOPHTHORA INFESTANS*) BY MEANS OF MYCELIUM DERIVED DIRECTLY FROM THE PLANTED TUBERS.

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II.

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It is now well over half a century since the potato blight became an epidemic disease in Europe. During the latter half of this period the practice of spraying the crop with some preparation of copper has become more and more prevalent as a preventive measure against this disease, until at the present time, in Ireland at least, spraying is generally regarded as an essential item in the cultivation of the potato crop, experience having proved its effectiveness and its necessity.

During the same period, however, comparatively little attention has been devoted to the extension of our knowledge of the fungus *Phytophthora infestans* which causes the disease; and we are not yet in a position to say that its life-history is completely known, although there are signs that the study of it is once more being resumed in earnest.

In one fundamental point, in particular, we are still almost completely in the dark, and that is as to the manner in which the potato-plants first become infected each succeeding season.

We do know that, during the summer, "spores" are produced which cause the spread of the disease from plant to plant during that season, but which are ephemeral, and are incapable of living over the winter from one season to the next. Judging from analogy, we should expect to find a second form of spore, formed sexually, and provided with a thick wall, and thus capable of living, probably in the soil, over the winter, and germinating in the following summer. If, however, we except Worthington Smith's work (2)[1] on this branch of the subject, which, although extremely suggestive, has not

[1] The numbers refer to the Bibliography at the end of the Paper.

obtained general acceptance at the hands of mycologists, and has up to the present not been confirmed by any other worker, success has not yet crowned the comparatively few efforts which have been made to discover such spores. Nevertheless, a more extended and patient search may even yet reveal them. The writer, for instance, has found spores in potato foliage destroyed by Phytophthora which, judged from a morphological standpoint, might easily be regarded as the oospores of this fungus, but which, although experimented with in very various ways over a period of six months, could not be induced to germinate, and so to reveal their nature. Resting-spores in this case, therefore, must be said to be unknown, but their existence is by no means improbable.

We also know with certainty that the fungus is found in the form of spawn, or mycelium, within the tubers, and that in them in this form it can pass the winter successfully; indeed, this is the only way, so far as we know at present, in which the fungus can live over the winter. Hence it would appear that, in the absence of resting-spores, diseased tubers must be the ultimate source from which the blight starts anew in any given season.

The question now arises as to exactly how infection of a new crop can occur from the diseased tubers of a former one. It is a well-known and easily demonstrable fact that the mycelium in diseased tubers produces at any time, provided the latter are placed in conditions of moderate warmth and moisture, a crop of "spores" on branched hyphae, which grow out from the tubers into the surrounding air. Should "spores" be produced from such a source above ground when the potato plant is in foliage, infection is likely to occur. Even if below ground, there is just the *remote* chance that such spores might be brought above it by the action of worms, &c. Hence particularly on small farms, where the newly planted crop will not be far away from last year's ground, or last year's pit, around which some diseased tubers are almost certain to be found lying about, there is some probability that infection may occur in this way. But since it seems probable that the chances of infection in this way are not sufficiently widespread to explain the constant recurrence of the blight, other possible sources of infection have been sought for, and recently the view that the potato plants become infected in the field directly from the planted tubers by means of mycelium, and not by "spores," has been revived; and the object of the present paper is to consider whether this view is supported by any substantial evidence and can be accepted as proved.

When a potato tuber is affected with Phytophthora, it shows certain characteristic external markings which proclaim the fact. Should there be any doubt in the matter, it is easy to induce the formation of the well-known

"spores," and settle it. When cut through, characteristic internal markings are also present, in the form of rusty-brown areas, confined in the earlier stages to the tissues near the skin. It is in these discoloured areas that the fungus mycelium is then to be found. If such tubers be carefully watched during the winter, it will be seen that the sprouts frequently begin to develop much earlier than on healthy tubers, as is also the case with tubers mechanically wounded, that the internal browning of the tissues gradually becomes more and more extended inwards through the tissues, and that the whole tuber becomes gradually destroyed. There is a race set up between the destroying fungus on the one hand, and the still-living part of the tuber on the other, and, in a very large percentage of cases, probably much more than half of them, the fungus gains the victory, and the tuber becomes entirely killed. On its surface, whitish pustules may often be seen, which, in some instances at least, are due to fungi other than that causing the blight. It is to be noted that there is little question of a resting period at all for the potato, and much less for the fungus. Both are active, although naturally the degree of activity depends to a certain extent on external conditions, particularly temperature. If this be raised, the activity is increased; if it fall, it is diminished. If the tuber wins the race, that is if it reaches planting-time, say in March or April, with some still healthy sprouts upon it, and a portion of its tissues still sound, this is largely because the attack was in the first place a slight one, or the tuber was perhaps large, and the distance from the attacked parts to the sprouts great, or possibly because it was kept at a comparatively low temperature, so that the fungus progressed but slowly.

To have reached planting-time with one or two sound sprouts, and a portion of the tuber still healthy, is, however, only the end of the first lap in the race. When such partially diseased tubers are planted in the soil, the moisture and warmth present there cause it to be resumed with renewed vigour. Experiments show that in a very large number of such cases no plant at all comes above ground, the tubers and their sprouts, if any, becoming completely killed before this is possible. In a few cases, however, the tubers do succeed in sending small shoots above ground, but these, after a very short time, succumb to the fungus which undoubtedly does grow up into them from the diseased tubers. In the remaining cases, contrary perhaps to what would be expected, the tubers, though originally diseased, give rise to what appear to be perfectly healthy plants, that is plants free from Phytophthora, although they may be somewhat less sturdy than plants grown from healthy tubers. Here, then, the potato plant has won the race against the fungus; for the sprouts develop and grow into healthy stalks, independent of the parent set

for nutrition, before the fungus has been able to invade them. Such plants, of course, may become attacked with the blight in the ordinary way by means of aerially borne spores later on.

Shortly summarized, therefore, it may be said of diseased tubers that they may—

(1) die before planting-time;
(2) die if planted in the ground, without producing any overground stalks;
(3) produce small stalks above ground which soon die owing to direct infection with the fungus from the parent tuber;
(4) produce healthy plants, which, provided there be no opportunity during the season of becoming infected by aerially borne "spores," remain free from the disease.

With regard to the tubers which are killed before planting-time, these can scarcely become a source of infection to the new crop. For, even if left lying about above ground, they will probably be no longer capable of giving rise to "spores" by the time that the new foliage has developed. The case of those tubers which are not actually dead at planting-time is, however, somewhat different. These, if too obviously diseased to be used as "seed," may be left lying about, and may still be capable of producing "spores" under suitable conditions when the new foliage has developed, and they would therefore be a source of danger to the ensuing crop.

Little danger is to be feared from any tubers which, being badly diseased, are planted and produce nothing above ground, for the chances of any "spores" which may have been formed on the tuber below ground finding their way in a living condition to the surface are but small. On the other hand, tubers which produce small diseased shoots above ground may be highly dangerous sources of infection, for on these shoots "spores" are produced which can easily be carried to neighbouring healthy plants.

There is, therefore, no question but that in a few cases the mycelium in a diseased tuber may succeed in reaching a shoot which has got above ground; but this takes place comparatively early, and such shoots are soon killed off. This early killing off of young shoots by invasion of mycelium from the tubers is, however, a very different thing from the supposed infection of well-grown plants by such mycelium some two or three months later in the season. If this actually occurs, the mycelium must be supposed to be growing with almost inconceivable slowness, or to be lying in a dormant condition during this period while these apparently healthy plants are developing. The recently propounded theory of mycelial infection to be discussed in this paper

involves the view that the mycelium becomes dormant for a period and then resumes its activity.

The chief advocate of the theory, which, on the face of it, as will be presently shown, has little to recommend it, is Massee (7), whose most recently published views may be summarized as follows:—When a diseased tuber is planted, the produce of such a tuber is always diseased; yet under certain conditions of weather (in bright, dry seasons) the stem and leaves of the plant may remain perfectly free from the disease. On the other hand, during a few cloudy, damp, sultry days in July the mycelium will take possession of the stem and leaves, which will succumb within a few days. The fact that simultaneous outbreaks of an epidemic may occur, extending over wide areas, is considered to be best explicable in this way.

According to this view, then, not only does the mycelium of Phytophthora lie dormant in the tubers during the winter, but also during the long period from planting-time—say, in March—until the time of the appearance of the blight in June or July. Incidentally it may be remarked that it is difficult to see how the *produce* of a diseased tuber can be diseased if at the same time the mycelium is lying dormant in the tuber; and the theory apparently states that, unless a season of unfavourable weather sets in, the stem and leaves remain free from the disease, and therefore in an exceptionally dry summer the *produce* from a diseased tuber would *not* be diseased!

My own observations of the behaviour of diseased tubers during the winter lead me to believe that even then the mycelium in them is not in a true state of hibernation or dormancy. During this period certain changes are going on; the tuber itself is slowly sprouting, and the mycelium invading fresh, healthy tissue at a rate depending largely upon the temperature at which the tubers are kept. But even if it is admitted that the mycelium in the tubers is dormant during the winter, it is almost impossible to entertain the idea that, when the tuber is planted, it still remains dormant. Surely planting the tuber in moist soil, which is also often considerably warmer than the surrounding air, would, if anything, encourage the mycelium to more active growth than before, rather than cause it to remain in, or take on, a latent condition! Another strong argument against the acceptance of this theory is that, according to it, the attack of the stalks must proceed from below upwards, whereas the exact contrary is what is actually found to take place in the fields. On healthy plants the blight always appears first as spots on the leaves or on the upper parts of the stalk or its branches, and never in the form of decay at its base. Even if the mycelium did lie dormant in the tubers, it must, to produce such spots, grow up through the stalks to reach such places; and how could it possibly do this

without affecting the tissues of the stalk and its branches? It is impossible to understand how this could occur without some indication of it being given by the wilting or other abnormal behaviour of the stalks and foliage, such as occurs in cases of Black Stalk Rot, Leaf Roll, &c.; but no such phenomena have ever been observed in the case of attacks by Phytophthora.

Anyone who is acquainted with the history of the numerous investigations which have been carried out on this disease during the past fifty years must know that experiments have proved that from diseased tubers perfectly healthy plants may be produced, which, provided they are kept free from all means of external infection by means of spores, remain unattacked throughout the season. Indeed, long ago the Prussian Government set the problem as to whether healthy or diseased plants were produced from diseased tubers, for solution to a body of scientific men on the staffs of its Agricultural Academies and Experimental Stations, with the result that it was found that diseased tubers produced healthy plants. Experiments carried out by Professor Carroll and the late Professor Wright at the Albert Agricultural Institution, Glasnevin, gave a similar result; and my own experiments, which will be dealt with presently, prove the same thing, so that there is no necessity to labour this point. And it is not impossible or even difficult to explain how this can be the case. Those who have studied and experimented with diseased tubers know how comparatively ephemeral the growth of Phytophthora on them is when they are kept in moist warm air, and how comparatively soon the growth of Phytophthora is over, and such tubers or pieces of them become swamped with growths of other fungi and bacteria, and become completely destroyed. When such a tuber is in the soil during the period from March till June or July, there is even more chance of this taking place. Meanwhile, however, the sprouts, especially if well started at planting-time, have developed into healthy stalks independent of the parent set.

Sufficient has now, I think, been said to show that, on *a priori* grounds, the theory of infection from dormant mycelium is a most improbable one. Hence it becomes necessary to examine carefully the evidence on which it is based. This, given in its chief upholder's own words, is as follows:—

"Three potatoes showing rusty stains in the flesh, indicating the presence of the mycelium of potato disease (*Phytophthora infestans*), were each cut into two equal parts. Each half potato was planted separately in a plant-pot, the soil and manure used being the same for all, and was sterilized by steam. Three of the pots were placed in a house having a temperature ranging between 70° and 80° F., and very often with moisture at saturation point. Each pot was covered with a bell-jar. The remaining three pots were placed

in a house without any artificial heat, and having the air exceptionally dry. These pots were not placed under bell-jars. An equal amount of water was supplied to each of the six pots. The stems and leaves of the three plants grown under conditions of high temperature and much moisture were attenuated and weak. The *Phytophthora* first appeared on these plants six weeks after planting; and a fortnight later all three plants were blackened and destroyed by the fungus. The potatoes grown in the cool, dry house were perfectly healthy when two months old. At this time one of the plants from the cool house was removed to the hot, damp house, and placed under a bell-jar. Within nine days this plant was completely blackened and killed by the fungus. A fortnight later a second potato plant, showing no indication of disease, was removed from the cool to the hot house, and placed under a bell-jar; within a week this plant was also killed by the *Phytophthora*. The third plant was allowed to remain in the cool house, and at the end of thirteen weeks, when the experiment ended, showed no trace of disease."

As a piece of scientific evidence in favour of the theory promulgated, this experiment is of course absolutely worthless, owing to the simple fact that no control plants derived from healthy tubers were used for purposes of comparison.

The details given of the experiment are unfortunately all too few. The time of the year at which it was carried out is not stated, nor is the mode of attack, whether from below upwards or from the foliage downwards, described. There is absolutely no evidence produced to show that the plants were not attacked by "spores" in the ordinary way. It is of course conceivable that the three plants in the warm house did become diseased from mycelium from the tubers; but six weeks is, in my experience, a longer interval than usually elapses in such cases. But even if they did, this occurrence has no bearing on the idea of *dormant* mycelium. With regard to the two plants brought to the warm house from the cool one, what could be simpler than to suppose that they became infected from "spores" previously produced by the first three plants? There is not a particle of evidence to show that they did not become attacked from this source; and the view that this may have occurred is strengthened by the fact that the single plant which was left in the cool house did not become diseased. There is a danger of laying far too much stress on abnormal weather-conditions as a necessity for the development of Phytophthora. For rapid growth and spread resulting in an epidemic undoubtedly a spell of warm moist weather is almost a necessity; but slow gradual development can occur under much less exacting conditions. I found, for instance, that infection and a comparatively slow but decided spread of the blight occurred on potted plants in an absolutely unheated greenhouse with a dry atmosphere even in the month of April, when the temperature

ranged from about 38° to 57° F.; and it is quite possible that the third plant mentioned above, and left in the cool greenhouse, remained healthy, not because the conditions were unfavourable, but merely because "spores" were absent. At any rate there is no evidence against this view.

Since the evidence in favour of the theory derived from the experiment described was of such an unsatisfactory nature, it seemed to me eminently desirable to carry out another one on similar lines, but with the addition of the absolutely necessary control plants. Starting in the early months of the year, in order to avoid any possible chance (at least in the early stages) of infection from aerially borne spores, I carried out an experiment of this kind which will now be described. I gladly avail myself of this opportunity of acknowledging with many thanks the assistance of my friend and colleague, Mr. F. W. Moore, M.A., Keeper of the Royal Botanic Gardens, Glasnevin, who was good enough to place at my disposal the necessary room in two of his glasshouses, and who afforded me other facilities for the work.

The experiment was started on February 11th, and brought to a conclusion on July 11th, 1910, and thus extended over five calendar months. Six potato-tubers of the variety "Champion" attacked by Phytophthora[1] were halved, thus making twelve sets in all. Six other tubers of the same variety, but perfectly healthy, were similarly cut into twelve sets. Twenty-four pots were filled with virgin loam which had not been previously used for potting purposes. Of these, twelve were sterilized by heating for half an hour each in an autoclave at 120° C., the remaining twelve being untreated. Six diseased and six healthy sets were then planted in the twelve pots of sterilized soil and the same numbers planted in the twelve pots of unsterilized soil. No manure of any kind was used. Of the twenty-four pots (twelve containing diseased sets and twelve containing healthy ones as controls) six were placed at once in a warm greenhouse, the temperature of which ranged from a minimum of 60° F. at night with fire-heat, up to 85° F. in the daytime with sun-heat, or at least 65° F. with fire-heat on cold days, and the atmosphere of which was fully charged with moisture, so that the conditions for the development of Phytophthora were extremely favourable. The soil in all these six cases had been sterilized, and three of the pots contained healthy sets, while the other three contained diseased ones. These pots were not covered at any time with bell-jars.

The remaining six pots of sterilized soil with three healthy and three

[1] Lest there should be any doubt in the matter as to whether these tubers were actually attacked by Phytophthora or not, it may be stated that I selected them personally from a severely diseased crop, and utilized the remainder of the batch not required for the experiment, for successful demonstration of the fungus, after suitable incubation, by the members of a large class of agricultural students.

diseased sets in them, together with the twelve pots of unsterilized soil containing six healthy and six diseased sets, were placed at the same time in a cool greenhouse with no artificial heat and with an exceptionally dry atmosphere.

As regards the three healthy (control) and the three diseased sets in the warm house, two of the latter produced overground stalks after twelve days, while the third one, although left for some considerable time longer, did not do so, and was found to have completely rotted away in the soil. A week later overground shoots were also produced from the three healthy sets, and these grew into large, perfectly healthy specimens, which were of course somewhat etiolated or "drawn," but which up to the end of the experiment never showed the slightest signs of Phytophthora or any other fungus on them. The plants from the two diseased sets also developed well, but in a slightly less robust fashion. One of them remained in every respect perfectly healthy and absolutely free from any form of disease whatever until the end of the experiment. The other one had but two stalks, one of which was very weakly from the start, but not owing to the presence of Phytophthora in it. After a short time one or two of the leaflets on this feeble stalk became blackened at their very tips. These leaflets were kept under close observation with the microscope, but only Botrytis developed on them, *not* Phytophthora. By degrees this feeble shoot gradually succumbed from above downwards. It was kept under close and constant observation; and when nearly dead it was removed and subjected to further microscopic observation and incubation, but not the slightest trace of Phytophthora was found on it at any time. The other stalk of this plant grew well, and remained entirely free from disease of any kind until the end of the experiment. Hence this part of the experiment resulted in the production of two plants absolutely free from Phytophthora from two diseased sets, placed under conditions extremely favourable to the development of this fungus.

Of the eighteen sets (nine diseased and nine healthy) in the pots in the cool greenhouse, most of the diseased ones produced overground shoots earlier than the healthy ones; but out of the nine diseased sets, three produced no plants, and were found to have completely rotted in the soil. All the nine healthy sets produced healthy plants. The plants developing from the diseased sets were here, as in the warm house also, somewhat less robust than those from the healthy ones, and one in particular (No. 15) produced a shoot only 2 or 3 inches high which quickly became diseased from below upwards, and soon died. Doubtless the mycelium had entered the shoot from the parent set. This plant was removed as soon as possible for fear of its causing the infection of the neighbouring ones by "spores." Up to April 27th all the plants in the cool house, with the above exception, had

diseased sets in them, together with the twelve pots of unsterilized soil containing six healthy and six diseased sets, were placed at the same time in a cool greenhouse with no artificial heat and with an exceptionally dry atmosphere.

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grown well and produced healthy foliage; but, on that date, suspicious-looking spots were seen on the leaflets of one of the plants grown from a healthy set. Microscopic examination showed that Phytophthora was present. The plant was removed immediately; but during the next few days Phytophthora gradually appeared in isolated spots on the leaves of seven of the plants from healthy, and four of the plants from the diseased, sets. These affected plants were removed immediately they showed signs of the disease; and by May 9th two plants only were left, one derived from a healthy, and one from a diseased, set. In view of the stress which is so frequently laid on the necessity of a high temperature and considerable moisture for the occurrence of Phytophthora, it may be regarded perhaps as somewhat surprising that the fungus should have developed and spread in this manner in a *cool* greenhouse during the month of April. The mean outside temperatures during the period in question were:—maximum 52·8° F., minimum 35·8° F.; and within the cool house they probably ranged from 57° F. to 38° F. Although absolute proof is lacking, it seems practically certain that the plants whose foliage became diseased must have become infected by means of "spores" from the single diseased sprout sent above ground by one of the diseased sets. There can be no question with these plants as to infection direct from the mycelium in the sets, for the attack began on plants derived from the *healthy* ones! It seemed hardly possible that the two plants left could have escaped contamination by "spores" like the rest and would remain free from disease for long; but yet during the period from May 9th to June 14th, extending therefore over more than five weeks, they were allowed to remain in the cool house, and no signs of Phytophthora made any appearance on either of them.

On the latter date after a final, most thorough search for any incipient signs of the blight, which gave an absolutely negative result, these two plants—one derived from a healthy and the other from a diseased set—were placed in the warm greenhouse mentioned above. Each of them was covered with a large bell-jar, and they remained under these conditions for a period of four weeks all but one day. During this time the bell-jars were occasionally removed for short intervals to permit of the thorough examination of the plants and to water the pots, which was but rarely necessary. So moist was the atmosphere within the bell-jars that intumescences were formed on the leaves of both plants; and such conditions must have been ideal for the development of Phytophthora. Nevertheless no signs of it ever appeared on the plants. As they grew, parts of some of the leaflets, chiefly their tips in both cases, came into contact at one or two points with the tops and sides of the bell-jars. Where this occurred the tissues decayed into a slimy material

in which bacteria were plentiful, but no Phytophthora was present; and all efforts to discover this fungus on either of these two plants during the period named met with absolutely negative results. This part of the experiment, therefore, confirms the previous part, the results being in both cases the production from diseased sets of plants entirely free from Photophthora under conditions extremely favourable to the fungus and withal adverse to the plant.

The result is the exact opposite to that obtained by Massee, who obtained diseased plants from diseased sets in five cases out of six; but, as pointed out above, in the absence of controls, it is impossible to assume with any degree of certainty that these plants became affected directly through the tubers. On the other hand, the result of my experiment is in agreement with those of many previous workers which are in the main to the effect that tubers affected with Phytophthora produce healthy plants; and the idea that the recurrence of the potato-disease year after year is due to the migration of dormant Phytophthora mycelium, in or into apparently healthy plants during unfavourable seasons of weather in the summer, can only be regarded as a theory with no evidence to support it.

During the summer the question of the production of healthy or diseased plants from diseased tubers was further tested at the Temporary Station for the Investigation of Plant Diseases at Clifden, Co. Galway. A single ridge of reclaimed bog-soil, occupying an area of about one square perch, was planted with 132 uncut "champion" tubers, attacked by Phytophthora, on April 12th. Only fifty-three of these produced plants; the remaining seventy-nine rotted in the ground without doing so. The fifty-three plants were not quite so robust as neighbouring ones grown from healthy tubers; but they showed absolutely no signs of Phytophthora until July 15th. On this date the blight was found as isolated spots here and there on the leaflets in the ordinary fashion, indicating an attack from spores borne from neighbouring plots, some of which were attacked with it three weeks earlier. It seems quite impossible to believe that these spots of blight, in many cases on isolated outstanding leaflets, could have arisen from internal mycelium, while the remaining portions of the plants, including the stalks, were quite healthy. How could Phytophthora, if present internally, have succeeded in carrying on an existence for over three months without exhibiting some signs of its presence? Even if it remained alive in the tubers all this time, which is to say the least most unlikely, how could it possibly have grown up through the stalks and out to the leaflets without leaving some impression of its strongly parasitic and destructive characters on the tissues through which it progressed? Comparisons have been made between the supposedly

dormant mycelium of Phytophthora, and that of some of the smut fungi; but such comparisons are entirely out of place until it has been definitely established that the former fungus does possess dormant mycelium, which is at present far from being the case. The general habits and behaviour of the smuts are so far removed from those of Phytophthora and its allies that the existence of any such similarity as is assumed is most improbable. The dormant mycelium theory is in reality but a modification of one brought forward in the first instance by de Bary, but discarded by him some five-and-thirty years ago as not being in accordance with known facts.

If this theory is correct, it seems almost impossible to explain the undeniably beneficial results accruing from spraying the crop with Bordeaux or Burgundy mixtures. Every grower of potatoes knows how essential it is to carry out this process of spraying *before* the blight has attacked the plants, for, if done later, the efficacy of the treatment is very seriously diminished. Spraying must be looked upon as a preventive method against the attacks of the blight from without and not from within. If the fungus once gains an entry into the tissues, external spraying does not prevent its spread in them. In some experiments which I carried out in 1909, I found that carefully painting over areas affected with blight by hand with Burgundy mixture, and even dipping affected foliage into the mixture, did not arrest the progress of disease, provided that the conditions of moisture and warmth were suitable. The mycelium of the fungus was even seen to emerge and form "spores" through places on leaves thickly coated and blue with the mixture.

Not only is this theory of dormant mycelium advocated to account for the infection of the over-ground parts of the potato-plant during the summer, but it is also employed to account for the attack of the new crop of tubers. It is stated that it has not been proved that the tubers become diseased as a result of the falling of the "spores" from the foliage on to the soil, and the ultimate arrival of them, or the products of their germination, on the surfaces of the tubers. It is strange that such a statement should be made at this time of day, in view of the many experiments which have been carried out to settle this point, and which force one to the conclusion that this in reality is at least the principal, if not the only, way in which the tubers *do* become infected.

If the new tubers are infected directly from the old ones by invading mycelium, why is it that those tubers nearest the surface of the soil, and therefore generally farthest away from the diseased set, become first and worse diseased than the deeper-lying ones? Why is it that the diseased areas of the new tubers are nearly always, if not always, superficial, and

are decidedly not in the majority of cases, as should be the case, situated at the "heel" end, where the rhizome enlarges to form the tuber? When the mycelium leaves the old set, and passes into the main stalk, and thence proceeds on its way to the new tuber (as it is supposed to do), why is it, as previously stated, that such stalk thus invaded at its base by a virulent parasite shows no signs of this in the drooping and other unusual behaviour of its foliage, as occurs in other similar cases such as Black Stalk Rot, &c.? The truth is that it is just as difficult to reconcile well-observed facts concerning the attack of the tubers with this theory as it is in the case of the stalks and foliage.

In the plot-experiment described above, the crop was raised on August 22nd, about five weeks after Phytophthora was first observed on the foliage. During this time the blight had not spread to any very great extent over the plot owing to the fact that the plants were sprayed three times, and when dug, they possessed but little diseased, and still plenty of healthy, green foliage. As was to be expected from the nature of the plants and the poverty of the soil, the yield was not a large one. All the tubers, however, were very carefully examined, and not a single one showed any traces of being attacked by Phytophthora. Being raised before the foliage was badly blighted, so that a copious fall of "spores" could not take place, it was to be expected that the tubers could scarcely have become infected from that source; but if they could become infected from the old sets direct, surely the period available for this to have occurred can scarcely be described as having been too short? For, if the hypothetical dormant mycelium had in this time been able to awake and reach the leaflets, surely it could have traversed the much shorter distance to the new tubers, and yet they were found to be healthy in every case!

It is further maintained that by means of this dormant mycelium theory the outbreaks of severe and simultaneous epidemics are more satisfactorily accounted for than by supposing that the destruction is due primarily to the dispersion of "spores." It is imagined that infection by this latter method would take place too slowly to permit of, say, the destruction of whole fields within a short period, as sometimes occurs. It is stated that "when a potato-plant infected with the spores of Phytophthora is placed under a bell-jar in a very damp atmosphere, subdued light, and high temperature—conditions most favourable to the development of the parasite—it is only after a period of four or five days that the fungus produces fruit on the leaves, and then only at the point of infection. On the other hand, the fact is too well known that a field of potatoes—or all the fields in a certain district—which at a given time appeared to be healthy

and vigorous have, under certain climatic conditions, been reduced to a blackened, decaying, fœtid condition within twenty-four hours.

Considering the second part of this statement, the whole of its import depends on the interpretation of the words "appeared perfectly healthy." If it is to be assumed that the words mean "*were actually* perfectly healthy," it is necessary to ask on what definite scientific evidence this statement rests, and the answer, I think, will be found to be—none! The first appearances of the blight are somewhat easily overlooked, even by trained observers, especially when a considerable area is under surveillance, for many of the attacked parts of the plant are more or less hidden by healthy foliage. Further, it is almost notorious how easily the early stages of attacks of plant-diseases in general are overlooked by farmers and others unless very special efforts are made to discover them. In all probability the words quoted are rather to be construed as meaning "seemed to be quite healthy to a casual observer," and, if this is so, epidemics are not by any means difficult to explain. It is quite easy to exaggerate the suddenness with which an epidemic comes on. What to a farmer might appear to be a sudden epidemic would be in many, if not all, cases to a trained observer nothing more than a rather quick culmination to a series of events which had been slowly proceeding beforehand more or less unobserved by others. The appearance of an epidemic is not frequently, if ever, absolutely contemporaneous with the advent of changed weather conditions; and my own observations lead me to believe that a serious spread of the disease occurs chiefly after a continuance of a few days of bad weather, rather than immediately on the setting in of it. Massee himself apparently requires a "spell" of bad weather for an epidemic to be set up.

As mentioned previously in this paper, too much stress must not be laid on special weather-conditions as a necessity for, at any rate, the slow production of "spores," and dissemination of the disease. It seems pretty certain, or at all events quite within the realms of possibility, that before an epidemic occurs, the blight is already present to some extent, more than one might be willing to admit, and that many of the leaves are spotted and bear "spore"-producing tufts of mycelium, while many others have "spores," which have fallen on them, in more or less advanced degrees of germination and infection. The advent of a spell of warm, moist weather has then, as a natural consequence, but not necessarily absolutely immediately, an alarming development of the disease. It may be that four or five days are required for infection resulting in fresh "spore"-production, to take place in artificial experiments; but it by no means follows that such a long period must elapse before the serious destruction occurs in nature, provided that

the external conditions are particularly favourable to the fungus, and that "spores" of various ages and in different stages of germination, and possibly of infection, are already fairly well distributed over the foliage. There therefore appears to be no really substantial reason for invoking the aid of this dormant mycelium theory in order to satisfactorily explain epidemics.

With regard to the spread of epidemics, Massee states:—"Again in the case of every fungus epidemic proved to be due to the diffusion of spores, the disease always originates from one or more primary centres of infection, and gradually extends, whereas in the case of the potato-disease the appearance of the epidemic is often simultaneous over a considerable area." It is true that in a given area the first appearances of blight are often observed at or about the same time in different places in that area, although where there are special cases of situation and exposure, exceptions to the general rule may occur. Now anyone who has carefully studied the question in the fields, or watched the development of the blight, knows that the disease does actually spread in them from such original centre or centres of infection exactly in the manner described; and during the past two summers I have had abundant opportunity of observing this in the clearest possible fashion. Let a period of warm, moist weather set in after a good, though to the ordinary person easily overlooked, start of the disease from such centres, and the occurrence of an epidemic needs no further explanation. Further, it must not be assumed that epidemics are indeed invariably simultaneous even over comparatively small areas, for I have observed in a field of potatoes of one variety, and all treated in the same way and not sprayed, one half suffering from an epidemic, while the other half has remained comparatively free from the disease.

Perhaps the most serious obstacle against accepting this dormant mycelium theory lies in the fact that, if it is to be used to explain epidemics in the manner suggested, it is almost impossible to get away from the suggestion that practically every potato which is planted is diseased with Phytophthora to start with. But the fact that a certain continental writer averred, a year or two ago, that there was no such thing as a healthy potato tuber in Europe, need not lead us as well to entertain such a ridiculous notion. In any case the said writer was probably not referring to Phytophthora, in particular, but rather to the disease known as Leaf Roll.

Enough has been said to show that this theory is based on no really scientific evidence, that it is extremely hard to reconcile with many of the well-known facts concerning the potato-disease, and that others of them can be satisfactorily explained without reference to it. Were its promulgation confined to scientific periodicals where its pros and cons could be adequately

discussed, little harm would be done. But where matter of this kind is incorporated as established beyond doubt into text-books written for the information of students and others, the case becomes more serious, owing to the danger of non-critical readers being misled.

There is no evidence at present existing to show that the attack of the potato-crop as a whole with blight occurs otherwise than by aerially borne "spores," if we except the few diseased plants from diseased tubers which do undoubtedly occasionally occur, but which can scarcely be regarded as being part of the general crop. Whether the sources of these "spores" at present known are sufficient to account for the annual recurrence of the blight, and particularly for the *time* of its appearance each year, are questions which must be left for future work to decide.

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