The 'Brown Rot' Diseases of Fruit Trees, with Special Reference to Two Biologic Forms of *Monilia cinerea*, Bon. I.

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With Plates XXV and XXVI.

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I. INTRODUCTION.

IT has long been common knowledge among horticulturists and plant pathologists that the fruits of the cultivated species of the genera *Pyrus* and *Prunus* are frequently attacked by fungi which, gaining access to the nutritious parenchymatous cells of the fruit through wounds or abrasions of the skin, rapidly develop within the tissues. The progress of the disease is indicated by a discoloration of the affected cells, the resulting brown colour often showing a striking contrast with the healthy tissues, particularly in the case of immature fruit with pale green skins (see Fig. 4).

The most important of the fungi producing these symptoms are to be referred to that genus of the 'Fungi Imperfecti' known as *Monilia*. Although these *Monilias* are able to continue from year to year without the interpolation of an ascigerous stage, such a stage has been observed, and it is now customary to allocate the species to the ascomycetous genus *Sclerotinia*.

The effect produced on the fruit by these species of *Monilia* is commonly known as 'Brown Rot' in this country, and this term is also now generally applied to the various diseases of fruit trees caused by these fungi. On the Continent the same diseases are referred to as 'Rot brun', 'Fäulniss der Früchte', 'Grind oder Schimmel des Obstes', 'Schwarzfäule', 'Blüten- und Zweigdürre', 'Muffa o marciume dei frutti', &c. The result of the development of the *Monilias* within the tissues is not usually, however, a 'rot' in the sense of putrefaction, since the organs attacked become so permeated with the mycelium that the whole forms a stromatic mass which generally tends to become more or less indurated rather than rotten. Thus the fruit, when so infected, instead of decaying and disintegrating, often becomes desiccated, and may remain on the tree in a 'mummified' condition for some months.

Towards the end of the nineteenth century serious losses to the cherry crops on the Continent, the flowers, fruit, and often branches being killed, led to an investigation of the cause of the outbreaks. The disease, at first attributed to the action of frost, was soon found to be due to epidemic attacks of a *Monilia*. It is now generally recognized that although the Brown Rot fungi are usually associated with fruit-rots they also cause blossom-wilts, destroy young twigs, and often kill branches by producing cankers which, girdling them and penetrating to the xylem elements, obstruct the course of the transpiration current and so cause the desiccation and death of those parts distal to the cankers.

The fruit is also liable to infection after it is picked, and apples in the store often suffer severely, for, since the disease under certain conditions is contagious, one affected apple may transmit the rot to those around it. Under storage conditions apples attacked by *M. fructigena* sometimes become quite black, a fact recorded in this country as early as 1885 by Worthington G. Smith.

That the Brown Rot fungi are recognized by mycologists and phytopathologists as of paramount importance is shown by the numerous papers and articles which have been published on the subject.¹ Many of these articles are merely records of the occurrence of the diseases, and relatively few supply scientific evidence for the conclusions arrived at. Of the experimental work, particularly that carried out on the Continent, very few investigators employed 'pure culture' methods in carrying out inoculations,

¹ See Bibliography on pp. 398-403.

and this, together with the fact that many workers still refuse to recognize that there are at least two distinct species of *Monilia* causing Brown Rot diseases, renders much of the work valueless as scientific records.

II. HISTORICAL.

In previous papers where the present writer (1917-18) described two specific diseases, on apple trees and plum trees respectively, literature was cited which related more particularly to the two diseases or to results obtained during the course of experiments connected with them, and no attempt was made to obtain a complete review of the papers dealing with those diseases of fruit trees caused by species of *Monilia*. Since the object of the present article is to show the relation which the two diseases bear to one another and to other Brown Rot diseases, a more general historical survey of our knowledge of the subject is desirable.

The earliest record of the occurrence of a *Monilia* on fruit appears to have been one by Persoon, who, finding a fungus producing tufts of moniliform chains of conidia on the decaying fruits of *Pyrus communis*, *Prunus domestica*, and *Amygdalus persica* in the year 1796, named it *Torula fructigena*. Five years later he changed the name to *Monilia fructigena*, and this is the name which is still usually applied to the conidial stage of the fungus. The former name was, however, frequently used for some time by certain workers, e.g. Albertini and Schweinitz (1805), Fuckel (1869), Saccardo (1873), Rabenhorst (1844-1853).

In 1817 Kunze and Schmidt named the fungus *Oidium fructigenum*, and this name was retained by Ehrenberg (1818), Fries (1829), Duby (1830), Cooke (1871), and Worthington Smith (1885). Other names by which it has been known are *Acrosporium fructigenum*, used in 1822 by Persoon himself, but not adopted by other botanists, *Oospora fructigena* and *O. candida*, as used by Wallroth (1833), and *Oidium Wallrothii*, by von Thümen (1875), who, however, in 1879 changed it to *O. fructigenum*.

Schröter, in 1893, from analogy with other species of *Monilia* producing an ascigerous stage, concluded that *M. fructigena* was the conidial stage of an ascomycete, and transferred it therefore to the genus *Sclerotinia*; in this connexion Prillieux (1897) wrote, 'ce n'est que par analogie que l'on peut regarder ce parasite comme une *Pezize* réduite à sa forme imparfaite de fructification'. In 1903 Ritzema Bos proposed that the fungus should be referred to the genus *Stromatinia*; this name has not been generally accepted, though adopted by Delacroix and Maublanc in their '*Maladies des Plantes cultivées*'.¹

The apothecial stage of *Monilia fructigena* was discovered on the Continent by Aderhold in 1904, thus confirming Schröter's conclusion regarding the ascomycetous nature of the fungus. Norton (1902) had two

¹ Loc. cit., vol. ii, p. 255. (Paris, 1909).

years previously found apothecia which had developed from mummied peaches; this form Norton himself referred to *Sclerotinia fructigena*, but Aderhold and Ruhland (1905) concluded that it was *S. cinerea*.

Westerdijk, in 1912, discovered a *Sclerotinia* on mummied cherries which, from the dimensions of its asci and ascospores, appeared to be different from *S. fructigena*, *S. laxa*, or *S. cinerea*; the direct connexion between the ascospores and a conidial stage was not traced however.

That *Monilia* was a genus which was to be considered as of economic importance was recognized by von Thümen in 1875, and in the following year by Hallier. Soon epidemic outbreaks of diseases caused by *Monilias* of fruit trees on the Continent resulted in the publication of many papers on the subject, particularly during the last decade of the nineteenth century, when articles appeared under such well-known names as Schröter (1893), Wortmann (1895), Wehmer (1895–6), Frank (1898), Frank and Krüger (1897–9), Aderhold (1897), Woronin (1897–9), Goethe (1898), Behrens (1898), Müller-Thurgau (1900), Sorauer (1899), and others,¹ the years 1897–1900 being prolific in references to epidemic outbreaks of *Monilia* diseases. In Germany the first serious complaint of such an epidemic appears to have been in 1894; thus Frank and Krüger write in 1899, ‘Die erste Klage über das epidemische Auftreten der Monilia-Krankheit... wurde in Deutschland im Frühling 1894 laut, wo die landwirtschaftliche Hochschule in Berlin über das allgemeine Absterben der Kirschenblüten in der Ortschaft Blankenfelde bei Berlin um Rat befragt wurde’.

Since 1900, Aderhold, Müller-Thurgau, and Sorauer have continued their observations, and others have taken up the work or recorded the damage caused, e.g. Ritzema Bos (1903), Molz (1907), Köck (1910), Muth (1910), Ewert (1912), Voges (1912), Westerdijk (1912), Broz (1913), and Eriksson (1913).

In 1818 Ehrenberg discovered a form on apricots which he named *Oidium laxum*; as with *O. fructigenum*, this fungus has also been referred to other genera, its synonymy being as follows:

Oidium laxum, Ehrenb. Sylv. (1818), p. 10, 22.

Acrosporium laxum, Pers. Myc. I (1822), p. 25.

Oospora laxa, Wallr. Flor. Crypt. (1833), n. 1574.

Monilia laxa, Sacc. et Vogl. Sacc. Syll. Fung. IV (1866), 35.

Sclerotinia laxa (Ehrenb.), Aderh. et Ruhl. (1905).

Aderhold and Ruhland (1905) found the apothecial stage of this fungus in 1904 developing from mummied apricots which had been placed in soil in pots and kept under observation; they cultivated the ascospores on artificial media and reproduced the conidial stage. Since that date the name *Sclerotinia laxa* has been generally reserved for the form producing

¹ See Bibliography.

the brown rot of apricots, e.g. Faes (1914), Chiffot and Massonnat (1915), Peglion (1917).

Bonorden in 1851 introduced the name *Monilia cinerea* for a form which he found 'auf faulenden Früchten'; as in the case of *M. fructigena*, Schröter, in 1893, referred it to the ascomycetous genus *Sclerotinia*.

In spite of Woronin's well-known papers of 1898-9, in which he submits convincing proof that *Sclerotinia fructigena* and *S. cinerea* can be readily distinguished even in the *Monilia* stage, other investigators refuse to accept his conclusions, and consider that 'Brown Rot' diseases of our cultivated fruit trees are caused by one species only, i.e. *S. fructigena*. Thus Frank and Krüger (1899)¹ say, 'Auch der von Woronin festgehaltenen Unterscheidung von *Monilia fructigena* Pers. und *M. cinerea* Bon. können wir wegen der Übergänge ihrer Merkmale nicht beistimmen, ein Standpunkt, auf dem auch Behrens und Wehmer zu stehen scheinen'. Eriksson (1913) also writes,² 'Ich mache hier keinen Unterschied zwischen *Monilia cinerea* und *M. fructigena*, da eine Speciesbestimmung nur nach der Farbe der Conidienpolster immer misslich ist'.

Although 'Brown Rot' has caused serious damage to the fruit crops in our own country for many years, no scientific investigations of the outbreaks have, until quite recently, been attempted, and references to the diseases have been practically confined to notifications of their occurrence and to the recommendation of methods of control adopted abroad. No attempt was made to compare the forms occurring here with those investigated by Woronin and others on the Continent, and generally it has been assumed that all outbreaks of 'Brown Rot' were caused by *Monilia fructigena*.³

In 1864 an article appeared in the 'Gardeners' Chronicle' over the initials M. J. B., describing a serious outbreak of a rot of apricots, the disease being caused by 'a little greyish mould, *Oidium fructigenum*'; a similar disease of apples and pears was assumed to be caused by the same fungus. Worthington G. Smith writes, in 1885, that 'The fungus (referred to *Oidium fructigenum*) is often extremely destructive to stored Apples when kept in damp or unventilated store rooms; the same pest destroys Pears, Plums, and other fruits.

'The warts are generally grey in colour, varying, however, in tint from cream to fawn colour, or different shades of grey.' It would seem from this description of the pustules that both *Monilia fructigena* and *M. cinerea* had been observed but not recognized as different species. The same writer had also noticed that 'The fungus has, in some instances, the power of changing the skin of the Apple to a jet-black colour'.

¹ Loc. cit., p. 203.

² Loc. cit., p. 65.

³ An article in the Gardeners' Chronicle of December 30, 1915, refers to *M. cinerea* and *M. laxa*, but only in relation to work done on the Continent.

Massee again recognized one species only, referring to it as *Monilia fructigena* in his 'British Fungus-Flora' (1893), and in 'A Text-Book of Plant Diseases' (1903); later (1910) he describes it as *Sclerotinia fructigena*. Cooke (1906) also attributed attacks of Brown Rot on apples, pears, cherries, and apricots to one species, *Monilia fructigena*.

Spinks (1915-16) has recently investigated 'A Black Rot of Apples', particularly with regard to its occurrence on cider apples, and finds that it is caused by *Sclerotinia fructigena*, in the restricted use of this name as defined by Woronin; this disease is probably identical with the one observed by Worthington Smith (1885).

In 1907 Salmon recorded outbreaks of Brown Rot on acid cherries, and in 1910-14 called attention to a serious 'Brown Rot' disease which destroys the blossom of apple trees and may invade the branches and produce cankers. The present writer (1917) undertook the further investigation of epidemic attacks of this 'Blossom Wilt and Canker Disease' of apple trees, which was particularly prevalent on the variety Lord Derby in the Weald of Kent, and found that the fungus responsible was not *Monilia fructigena*, which had been assumed to be the species causing the disease, but a grey *Monilia* conforming to descriptions of *M. cinerea*, Bon. Later a 'Wither Tip of Plum Trees' (1918) was found to be caused by a fungus morphologically similar to that occurring on 'Brown Rot Cankers' of apple trees, but was different from that form biologically, in that it was unable to establish itself in the flowering spurs of the apple, and so was incapable of inducing the typical 'Blossom Wilt' condition or of forming cankers on apple trees.

Meanwhile phytopathologists in the United States had been attracted to the investigation of outbreaks of 'Brown Rot' in America, where fruit-growers were subjected to great losses annually, caused by a species of *Monilia*, peach trees proving particularly susceptible to the disease. Peck (1881) found that *Oidium fructigenum* attacked the fruit through wounds, for he was unable to produce infection by placing conidia on the uninjured skin. In 1886 Arthur recorded a blossom infection of cherries in New York as having occurred during the previous summer, and three years later Erwin F. Smith (1889) described a blossom blight of peaches as caused by *Monilia fructigena*, another paper on the same subject by the same author appearing in 1891. In that year Humphrey also wrote on 'The Brown Rot of Stone Fruits', and he too referred the fungus to *M. fructigena*, which he believed to have a conidial stage only. During the nine years following, further papers by Humphrey appeared, and other investigators took up the work, e.g. Chester (1892), Taft (1894), Bailey (1894), Goff (1897), Quaintance (1900), Waugh (1900).

In 1902 Norton made an important discovery when he found the ascigerous stage of the Brown Rot fungus occurring on peaches in Maryland;

the apothecia were developing from mummied fruit which had been lying on the ground for some time in an old peach orchard. Many bulletins on Brown Rot appeared during the succeeding ten years, dealing chiefly with the therapeutics of the disease, which was still generally attributed to *Monilia fructigena*. Then a series of papers appeared, written by Jehle (1913), Matheny (1913), Cooley (1914), Conel (1914), Valteau (1915), Brooks and Fisher (1916), and Bartram (1916), in which the writers conclude that the Brown Rot organism occurring in America is identical with *Monilia cinerea*, Bon., of Europe. ‘Peach Canker,’ attributed by Jehle to *Sclerotinia cinerea* (1913) or *S. fructigena* (1914), is found by McCubbin (1918), working in Ontario, to be due mainly to *Valsa leucostoma*, though the initial lesions in many instances are caused by the ‘Brown Rot fungus’.

The Brown Rot diseases are also common in Australia,¹ and in New Zealand, as shown by Mansfield (1916), Cockayne (1918), and Cunningham (1918).

Articles recording experiments bearing on the physiological activities of fungi frequently give some attention to the Sclerotinias of fruit trees, e.g. Behrens (1898), Schellenberg (1908), Bruschi (1912), Cooley (1914), and Brooks and Cooley (1916).

III. GENERAL OBSERVATIONS.

In addition to observations already recorded in reference to a ‘Blossom Wilt and Canker of Apple Trees’ (1917), and a ‘Wither Tip of Plum Trees’ (1918), examination of diseased fruit trees in various districts of Kent, and of specimens received from other sources, has yielded further interesting information relative to the occurrence and mode of parasitism of *Monilia cinerea* and *M. fructigena*, and the following notes supplement those records of observations in the open which have already been published.

(a) The Occurrence of *Monilia fructigena* and *M. cinerea* on *Prunus* spp.

It has been generally assumed that *M. cinerea* is wholly, or almost, restricted to the stone-fruit trees (*Prunus* spp.), and *M. fructigena* to species of *Pyrus*. This assumption has arisen from the observations recorded by continental workers, and does not necessarily obtain in this country; in fact, *M. fructigena* is often found on cherries and plums, while a form of *M. cinerea* is responsible for a serious Blossom Wilt of apple trees. The records of the occurrence of *M. cinerea* on stone-fruit trees on the Continent have been chiefly in reference to the disease on the ‘Sauerkirsche’. The acid cherry trees grown in England are also very susceptible to attack from *M. cinerea*, the blossom, fruit, and branches being killed; in no instance have I found *M. fructigena* on the acid cherry. In Kent the sweet cherries

¹ Vide McAlpine’s ‘Fungus Diseases of Stone Fruit in Australia’, p. 53. Melbourne, 1902.

are cultivated on a much greater scale than the acid cherries, and on these *M. fructigena* is frequently found on the ripening fruit, while *M. cinerea* not only occurs on the fruit, but may sometimes cause a serious Blossom Wilt, as in the spring of 1918.

Both species are found on ripening and mature plums; sometimes *M. cinerea* is the predominant species present, on other occasions *M. fructigena*. In 1916 two growers, one in Sussex, the other in the Maidstone district of Kent, complained of serious losses by Brown Rot at the time of picking; samples sent to Wye College were found in each case to be affected by *M. fructigena* only. On the other hand, an orchard of Czar and Bush plums, near Maidstone, visited by the writer at the time the fruit was being gathered in 1917, was found to be infected by *M. cinerea* almost exclusively, a few examples only being found with *M. fructigena*. In another orchard, plums (varieties Monarch and Victoria) were attacked by the two species almost equally; in some instances the same cluster of plums bore both species, and occasionally the two were found on one and the same plum (see Figs. 1 and 2).

Both species occur on damsons, *M. cinerea*, as far as my own experience goes, being the more frequent. On peaches I have found *M. fructigena* on the ripening fruit and *M. cinerea* on dead twigs, but have not yet met with apricots affected with Brown Rot.¹

(b) *The 'Wither Tip' Disease of Plum Trees in 1918.*

This disease, which was prevalent in Kent in 1916, was practically absent in the following year, but reappeared with its former intensity in 1918, when it was again (as in 1916) associated with an attack of aphides (*Aphis pruni*). Specimens of the 'Wither Tip' disease, received from Worcestershire and Norfolk, also bore traces of aphides on the leaves. The simultaneous occurrence on plum trees of the attack by the aphid and the outbreak of the *Monilia* disease of the vegetative shoots lends support to the theory that the insect renders the trees more susceptible to 'Wither Tip', either by aiding the dispersal of the conidia, by carrying them from one shoot to another, or by so injuring and weakening the leaves by punctures that the fungus is able to invade the tissues of the leaves and then the shoots; probably both these factors are operative during a severe infection.

Observations in 1916-17 proved that on diseased shoots infected in 1916 pustules of *Monilia cinerea* appeared during the following winter and spring. An examination of the same twigs (which had been labelled on the trees) in 1918 showed that pustules with viable conidia were again to be found on some of them, though many bore no fertile pustules at that time. Such twigs, therefore, may serve as sources of infection for two years.

¹ While this paper was in the press apricot twigs, bearing a fungus morphologically identical with *M. cinerea*, have been received at Wye from Norfolk.

(c) *Sources of Infection on Plum Trees.*

It is only during years of abnormal weather conditions, such as obtained in the spring of 1918, that heavy losses are produced on sweet cherries by the Brown Rot fungi. The plum tree, however, proves generally to be more susceptible, and each year extensive damage to the crop is reported. *Monilia fructigena* appears to be confined to the fruit, and persists from year to year, so far as is at present known, only on the mummied fruit, in this country. *M. cinerea*, on the other hand, not only attacks the fruit, but also the flowers, leaves, young shoots, and branches, thus not only directly reducing the cropping powers of the tree, but providing numerous sources of infection for the developing fruit.

From observations made at Wye it was found that at the time the fruit is about half grown, pustules of *M. cinerea* may be found on

- (1) mummied fruit, the result of infection during the previous year ;
- (2) flowers killed in the spring of the current year ;
- (3) newly-attacked leaves on the vegetative shoots of the current year ;
- (4) vegetative shoots killed during the previous year ;
- (5) cankers formed the previous year on the branches.

The 'Wither Tip' condition may occur also on the 'suckers' at the base of the trees, and on those shoots growing out from the stumps of trees cut down ; these serve as sources of infection which may easily escape observation.

(d) *An Epidemic Outbreak of a 'Blossom Wilt' of Plum and Cherry Trees in 1918.*

In 1918 the yields of the plum and cherry crops were far below the average. From investigations made in Kent it appeared that the failure was largely due to *Monilia cinerea* aided by weather conditions particularly favourable for the dissemination and development of the fungus during the period when the trees were in bloom, the atmosphere being almost continually saturated with moisture for about a week. The following factors contributed in inducing the epidemic outbreak of the disease :

(1) The low temperature retarded the development of the flowers, which on opening remained receptive and liable to infection for a relatively long period ; this was partly owing to the fact that the cold wet weather decreased the activities of pollinating insects.

(2) The successive expanding of the flowers extended over a period long enough for those primarily infected to produce pustules of conidia during the time that later flowers were in progress of opening ; these flowers which expanded towards the end of the flowering period were

therefore liable to infection from two sources, viz. mummied fruit and infected flowers.

(3) The pustules borne by the mummied fruit became extremely pulverulent with conidia (the saturated atmosphere being particularly favourable for their development) during the period when the flowers were open.

Another important factor was the great fertility of the trees during the previous season, in consequence of which many plums and cherries had remained unpicked and had become infected with *Monilia*, with the result that they persisted on the trees as ‘mummies’ and served as the primary source of infection during the spring of 1918.

(e) *Monilia cinerea* and *M. fructigena* on *Pyrus* spp.

The assumption that *Monilia cinerea* rarely occurs on the ‘cored fruit’ has been negatived during recent years, the fact that this species may frequently cause the destruction of 50 per cent. to 75 per cent. of the inflorescences of certain varieties of apple trees and that it is generally distributed throughout the fruit-growing counties in the south of England being sufficient evidence that on those varieties of apple trees it is far more dangerous than *M. fructigena*. The latter species occurs almost exclusively on the fruit, but occasionally extends from the infected apple into the fruiting spur (Fig. 3) or even into the branch to form a canker (Fig. 14). *M. cinerea*, on the other hand, infects the flowers and, rapidly advancing into the spurs, kills them, and cankers, girdling the branches, are often produced (see Figs. 10–13). The statement made in 1917 that I had never found *M. cinerea* on maturing or ripe apples still holds good.

With reference to the Brown Rot Canker disease, earlier observations appeared to show that the fungus produces fructifications on spurs and cankers during the winter and spring following their infection, and that subsequently the fungus produces no more pustules, but dies away, and the cankers become covered by the development of callus (see Fig. 16). More recent observations have shown that, although this is true as a general rule, in some instances infected spurs have developed pustules during the second year after infection. Thus in the summer of 1917 it was found that a few of the spurs labelled as being infected in 1915, and which had produced pustules in 1916, also bore pustules in 1917; in one instance a spur which had been infected from artificial inoculation of the inflorescence from a pure culture in 1916, and had borne fructifications in 1917, produced still other pustules with viable conidia in 1918, though the canker which had been formed at the base of the spur was by this time almost healed over by callus (see Fig. 13, which shows the spur and canker here referred to, photographed in March, 1918). In every case observed where a canker has been produced that has not completely girdled the

branch the lesion tends to become healed quite early (Fig. 16), and no more pustules develop on the cankered surface of the branch itself subsequent to the year following infection. When, however, the canker girdles and kills the branch the lesion cannot be healed and the fungus may persist in the tissues of the canker for several years. In the spring of 1917 large cankers bearing numerous pustules were removed from affected trees; some of these were placed in a pot on the ground, others were suspended at about 3 feet above the ground level. In January, 1919, those cankers which had been suspended still bore numerous powdery pustules (see Fig. 12); of those on the ground most had lost their bark and no pustules were present, while the rest bore a few pustules at the upper end. Such cankers, therefore, may serve as sources of infection for at least three years.

Another feature, not previously recorded, in connexion with this disease is the fact that when a leading branch is girdled by a canker, which, as already shown,¹ occurs about the end of June when the tree is growing vigorously, the upward flow of sap is suddenly checked and diverted into the buds immediately below the canker, with the result that these buds are stimulated to grow out into weak vegetative shoots instead of developing into fruiting spurs (Fig. 15). A similar result has been described and figured as occurring on plum trees affected with the 'Wither Tip' disease.² On pear trees I have met with *Monilia cinerea* on one occasion only, when it was found on a young pear about 1 cm. in length, while *M. fructigena* often occurs, causing a brown rot, on the ripening fruit.

Pyrus japonica is subject to a Blossom Wilt similar in general appearance to that of the apple tree. I have isolated the fungus in one case, and it proved to be similar physiologically and biologically to the form of *M. cinerea* obtained from plums and cherries.

IV. METHODS ADOPTED IN ISOLATING PURE STRAINS.

The strains of *Monilia* used in the experiments recorded in this paper were all 'pure', each being derived from a single conidium; the conidia were obtained for this purpose either directly, from naturally infected specimens bearing fructifications, or indirectly from cultures prepared with the object of inducing the development of conidia in those cases where mycelium only was present in infected material.

A method of isolating pure strains of *Monilia* from infected tissues containing mycelium has been described in previous papers (1917-18), and brief references have there been made to a method of obtaining strains from single conidia. The latter given in detail is as follows: Two watch-

¹ Vide Ann. Appl. Biol., vol. iii, p. 167.

² Vide *ibid.*, vol. v, Plate VIII, Fig. 3.

glasses, held in forceps, are passed several times through a Bunsen flame; one is then inverted over the other and both allowed to cool, when into the lower is poured about 1 c.c. of sterilized distilled water. Particles of pulverulent pustules are brought in contact with the water, and the conidia, becoming detached, float on the surface. By means of a flamed platinum wire loop (1 mm. diam.) drops are transferred from the watch-glass to the surface of sterilized nutrient agar in a Petri dish. As this operation is carried out in a room set apart for culture work it was found possible to examine these drops directly, the cover of the dish being removed, under a low power of the microscope with but little risk of contamination. Since the conidia float on water the surface of the drop is brought into focus and examined for the presence of floating conidia. Generally with one loopful three drops of water can be deposited on the agar without recharging the loop, and this is a convenient number to examine before evaporation causes their obliteration. When a drop is found to contain a single conidium the cover of the dish is replaced and a ring of ink is made on the bottom of the dish to mark its position. Several such marked drops having been obtained, the dish is placed in a drawer at room temperature until the following day. After twenty-four hours the inverted plate is examined under the microscope with a 1-inch objective. One of the rings of ink is brought into the field and the microscope tube is gradually lowered until the agar is in focus as indicated by the appearance of numerous small granules; the layer of granules last seen before they disappear from view indicates the surface of the agar, and this is then examined at that level for the germinating conidium within the ring of ink, the blurred outline of which is still discernible.

It will, in general, be seen at this stage whether the conidium is truly isolated or whether contamination has taken place. In most instances the length of the germ tube and its mode of growth were also noted, and it was generally found that the germ tube of *M. fructigena* could be distinguished from that of *M. cinerea*.¹

On the second day after isolation they are again examined and two or three of those which are found to be uncontaminated, and quite isolated from other germinating conidia, are transferred to another agar plate. Usually this transference is made after forty-eight hours, but occasionally, when the temperature of the room was low and growth had not been vigorous, the sporelings were removed on the third day after the isolation of the conidia. When the resulting mycelial discs are 2–3 cm. in diameter (representing about eight days' growth) small portions of the mycelium are removed from the periphery of the disc and placed on agar slants in test-tubes for future use, and when conidia are required sub-inoculations are also made on sterilized potato.

¹ Further details will be given in Part II of this paper.

In this way purity of culture is ensured, for should contamination arise from fungus spores, or by bacteria capable of growing on the culture medium employed, it would be detected during the forty-eight hours succeeding isolation, and should the sporeling be contaminated by bacteria which do not develop under those conditions and would therefore escape detection, they are eliminated by taking mycelium from the peripheral region of the mycelial disc after growth has proceeded for a few days. This method was the one adopted for obtaining the 'single spore strains' of *Monilia fructigena* and *M. cinerea* (used in the experiments described in this paper) when viable conidia were available, i. e. when the fungi were developing pulverulent pustules.

When the parasites occur as barren mycelium in the tissues of the host they are induced to produce conidia on sterilized potato as already described in the papers on 'A Blossom Wilt and Canker of Apple Trees'¹ (1917) and 'A Wither Tip of Plum Trees'² (1918). The conidia are then isolated and single spore strains obtained as described above.

Single spore strains of *Monilia fructigena* were prepared directly from the conidia of fertile pustules on apples or apple spurs, or indirectly from barren pustules (winter condition) by placing particles of the pustules on the nutrient agar, thus inducing vegetative growth for sub-inoculation on potato for conidia production. 'Black Rot' strains of *M. fructigena* were also obtained indirectly by first stimulating vegetative development from particles of the diseased apple flesh (permeated with mycelium) placed on the agar.³

V. INOCULATION EXPERIMENTS WITH *MONILIA CINEREA* AND *M. FRUCTIGENA*.

(a) Apples inoculated with Strains of the Two Species.

Experiments carried out on apples in 1916 with the object of comparing the action of that form of *Monilia cinerea* which causes the Blossom Wilt disease of apple trees with that of a strain of *M. cinerea* isolated from a plum affected with Brown Rot, and with that of a strain of *M. fructigena* also obtained from a plum, have already been described in a previous paper (1917). It was there shown that the mode of development of the Blossom Wilt form of *Monilia* under those conditions (growing on immature apples in the laboratory) was different from that of either of the other two forms in that the brown coloration of the affected areas rapidly became dark brown and finally black in the case of the Blossom Wilt strain, while the

¹ Loc. cit., p. 174.

² Loc. cit., p. 33.

³ The writer has found the method here described (slightly modified in the case of spores or conidia which do not float in water) of obtaining 'single spore strains' suitable for other fungi with reproductive bodies large enough to be easily seen under a low power of the microscope.

other two strains failed to induce this nigrescence except on fully matured apples inoculated some time after they had been picked and stored; it was also to be distinguished from the fact that on the apples so infected it produced very few pustules, or in some instances none at all, while the strains of *M. cinerea* and *M. fructigena* from plums readily developed pustules.

During 1917 another series of experiments was carried out using the same strain of the Blossom Wilt fungus (which, however, had been re-isolated from an apple spur infected from a pure culture) and other strains of *Monilia cinerea* and *M. fructigena*. In this series, Experiments Nos. 4 and 5 were made on apples growing on a tree in the open, Nos. 1, 2, 3, 6, and 7 on apples which were inoculated and kept under laboratory conditions. In the latter case, the fruit after inoculation was placed in a glass vessel which had been sterilized on the inside by a thorough cleansing with cotton-wool soaked in 95 per cent. alcohol. The actual inoculation consisted in making a small V-shaped cut through the skin, removing a particle of the tissues underneath, and inserting mycelium from an agar culture of the fungus, the skin being then turned back into position. When the resulting 'Brown Rot' had developed for about seven days, by which time the fungi had become well established in the tissues, the apples were placed under bell-jars on a slate slab (which had also been cleansed with alcohol), the jars being raised above the surface of the slab on glass supports 1 cm. in height, thus allowing for a circulation of the air. This method, though not excluding the possibility of infection by other organisms during the latter stages of the experiment, provided conditions less abnormal than would have been the case had the apples been kept in an enclosed space throughout the experiment, and as no other organisms appeared it is to be concluded that the results obtained were produced by the fungi inserted in the wounds.

In 1917 inoculation experiments on apple flowers showed that the strain of *Monilia cinerea* obtained from a 'withered tip' of a plum tree was unable to induce the Blossom Wilt condition on the flowering spurs of the apple; other experiments carried out in 1918 (described in detail in the present paper) with other strains from plum and cherry also failed to produce the Blossom Wilt on apple trees. The 'Blossom Wilt and Canker' form of *Monilia cinerea* is therefore distinct biologically from that occurring generally on the species of *Prunus*, and it is proposed, for convenience, to refer to it in describing the following experiments as *Monilia cinerea* forma *mali* and the form on plum and cherry as *M. cinerea* forma *pruni*. Strains of *Monilia* obtained from America have also been used, and, as these have certain characters in common which distinguish them from *M. cinerea* as found in Europe,¹ they will be referred to as *M. cinerea* forma *americana*.

¹ Vide Ann. Appl. Biol., vol. iii, No. 4, p. 180.

EXPERIMENT 1.

Strains used $\left\{ \begin{array}{l} \textit{Monilia cinerea} \text{ forma } \textit{mali}. \\ \textit{M. fructigena}, \text{ strain from apple spur.} \end{array} \right.$

Two apples (var. Bramley's Seedling) were each inoculated on one side with a strain of the apple Blossom Wilt form of *Monilia cinerea*, and on the opposite side with a strain of *M. fructigena* obtained from an apple spur which had become infected through the fruit. The inoculations were made on September 14, 1917, with the following results:

September 21. In both apples on the side inoculated with *Monilia cinerea* the rot had extended 2.5–4.5 cm. from the point of inoculation; no pustules were present, but conidiophores had developed along the cut at the place where the inoculation was made; the discoloration was a deep brown, with darker, more or less concentric zones; many of the lenticels were marked with dark circles.

On the side inoculated with *M. fructigena* the rot had extended 3–3.5 cm.; a few yellow pustules, to 2 mm. in diameter, were present, and conidiophores had also developed along the wound; the discoloration of the surface was a bright brown, except in the immediate neighbourhood of the point of inoculation, where the colour was darker for about 1 cm.

October 12. *M. cinerea* had extended through about two-thirds of each apple, the surface on that side being *black* in colour; the skin was hardly shrunk and bore no pustules. *M. fructigena* had made less progress, about one-third of the surface being affected; the skin was *bright brown* in colour, much shrunk, and bore numerous yellow pustules.

October 25. There was no further change except that the shrinkage was more pronounced, particularly on the side infected with *M. fructigena*.

These results were essentially the same as those obtained in 1916, when a strain of *M. fructigena* obtained from a plum had been compared with the Blossom Wilt form of *M. cinerea* (see Figs. 4 and 5).

EXPERIMENT 2.

Strains used $\left\{ \begin{array}{l} \textit{Monilia cinerea} \text{ forma } \textit{mali}. \\ \textit{Monilia cinerea} \text{ forma } \textit{pruni}. \end{array} \right.$

Two apples were each inoculated on one side with the apple Blossom Wilt strain used in Experiment 1, and on the other side with a 'Wither Tip' strain of *M. cinerea* from a plum tree. The inoculations were made on September 14, 1917.

RESULT.

	Sept. 21.	Oct. 12.
Apple No. 1 on side inoculated with <i>M. cinerea</i> forma <i>mali</i> .	Discoloration extending 4-4.5 cm. from inoculated wound, dark brown in zones, no pustules present, conidiophores along cut	A little more than half the surface of the apple <i>black</i> , not shrunk; no pustules, but a few small barren papillae present.
Apple No. 1 on side inoculated with <i>M. cinerea</i> forma <i>pruni</i> .	Discoloration extending 2.5-3 cm., from wound, bright brown with a slightly darker margin; a few minute scattered pustules.	This side (rather less than half surface) <i>brown</i> and distinctly marked off from the black portion; not shrunk; no powdery pustules, but numerous papillae present.
Apple No. 2 on side inoculated with <i>M. cinerea</i> forma <i>mali</i> .	Discoloration extending 4-6 cm. dark brown in zones; a few small scattered papillae; conidiophores along cut.	As in Apple No. 1.
Apple No. 2 on side inoculated with <i>M. cinerea</i> forma <i>pruni</i> .	Discoloration extending 1.5-3 cm. from wound; many small pustules present and conidiophores along the cut.	Numerous small grey pulverulent pustules present; skin distinctly shrunk and wrinkled, <i>brown</i> .

October 25. No further definite change in any of the apples except that the shrinkage is a little more pronounced.

The two strains used in this experiment were the same as those used in the inoculation of apple flowers as described in the paper on 'A Wither Tip of Plum Trees' (1918); in that paper it was shown that the Wither Tip strain failed to induce the typical 'Blossom Wilt' condition on an apple tree, while on the same tree inflorescences inoculated with the Blossom Wilt strain quickly succumbed. In the case of these two strains the degree of the virulence of their parasitism on apple flowers is associated with differences in their physiological relations with the host tissues when growing on the fruit of the apple tree.

EXPERIMENT 3.

Strains used—*Monilia cinerea* forma *mali*.
Monilia cinerea forma *pruni*.
Monilia cinerea forma *americana*.
Monilia fructigena, strain from an apple spur.
Monilia fructigena, strain from a 'Black Apple'.

Fifteen apples (all of one variety, viz. Bramley's Seedling) were selected as being free from blemishes, divided into groups of three, and the groups respectively inoculated with the five strains of *Monilia*. The strains of the forms *mali* and *pruni* of *M. cinerea* were the same as those used in Experiment 2, and the strain of *M. fructigena* obtained from an apple spur was that used in Experiment 1. The present experiment, therefore, served as a duplicate of the previous ones, and also introduced for com-

parison the American form of *M. cinerea* and a 'Black Apple' strain of *M. fructigena*.

The apples were inoculated on October 26. 'Brown Rot' soon appeared in all of them except one of those inoculated with the 'Black Apple' strain of *M. fructigena*, and as, with this exception (in which infection failed), the results obtained in any one series were approximately uniform, they are described in the table in general terms.

RESULT.

Strain of <i>Monilia</i> .	Nov. 3.	Nov. 30.
<i>M. cinerea</i> f. <i>mali</i> .	The rot had extended 2.8-4.0 cm. from point of inoculation; pustules absent; distinct but irregular dark brown zone at 1.5-2.5 cm. from the wound.	One apple quite black, the other two black over nearly the whole surface, the remaining portion being dark brown; pustules minute, few in number; skin very slightly wrinkled.
<i>M. cinerea</i> f. <i>pruni</i> .	Extension of rot 2.2-3.5 cm.; numerous grey pustules on one apple and a few on the others.	Surface of all three a bright brown; no nigrescence except for a few millimetres immediately round the wound; numerous grey pustules about 1 mm. diam.; skin much shrunken and wrinkled, particularly where the pustules were closely aggregated.
<i>M. cinerea</i> f. <i>americana</i> .	Extension of rot 2.0-3.0 cm.; discoloration brown, with a darker zone at 0.5-1.0 cm. from wound; pustules few, small (about 1 mm. diam.), and grey.	All three quite black with the exception of a small brown patch on one of them; pustules few, small, grey; skin slightly wrinkled.
<i>M. fructigena</i> . Strain from apple spur.	Extension of rot 1.8-2.5 cm.; pustules absent; discoloration brown, with a narrow peripheral zone a little darker.	All three brown to dark brown; pustules yellow, to 3 mm. diam., very numerous; surface of apples much shrunken and wrinkled.
<i>M. fructigena</i> . Strain from a 'Black Apple'.	Extension of rot 1.5-2.7 cm.; pustules absent; discoloration brown, with a narrow peripheral zone a little darker.	All three brown to dark brown; pustules yellow, to 3 mm. diam., very numerous; surface of apples much shrunken and wrinkled.

EXPERIMENT 4.

Strains used { *Monilia cinerea* forma *mali*.
 { *Monilia fructigena*, strain from an apple spur.

On July 6, 1917, six apples (var. James Grieve), growing in the open, were inoculated with *M. cinerea* and eight with *M. fructigena*; a number of apples wounded but not inoculated served as controls. In each series infection failed in two of the apples. Those which became infected had all fallen by July 20, so that it was decided to repeat the experiment, and other apples were inoculated with the same strains on July 24, as described under Experiment 5. The results obtained to July 20 are to be noted, however, for comparison with those recorded in the next experiment.

The apples infected with *M. fructigena* became within eight days discoloured over more than half the surface; in one case the whole surface was brown. At this stage a pale raised circular pustular zone, covered by the epidermis, had developed at approximately 1 cm. from the point of inoculation; a few days afterwards yellow pulverulent fructifications of *M. fructigena* burst through the skin in that zone, and later numerous pustules appeared on the rest of the surface.

Of the apples infected with *M. cinerea* two had become discoloured over three-fourths of the surface, the other two over the whole surface, but no pustules had developed.

In both series the apples in which inoculation had failed to produce infection were still on the tree on July 20, as were also all the control apples.

EXPERIMENT 5.

Strains used { *Monilia cinerea* forma *mali*.
Monilia fructigena, strain from an apple spur.

This experiment was carried out on apples (var. James Grieve) growing in the College plantation. The apples were inoculated on July 24 by making in each a single puncture with a sterile needle, and inserting in the puncture a particle of a pustule obtained from a pure culture of the fungus growing on sterilized potato. Ten apples were inoculated with each of the two strains, and, to serve as controls, ten apples were punctured but not inoculated.

RESULT.

	July 26.	July 30.
<i>M. cinerea</i> f. <i>mali</i> .	Rot had commenced in all the apples, the brown areas round the punctures varying from 3 to 13 mm. in diameter.	About half the surface of each was discoloured; four of the apples bore no pustules whatever, four had a few scattered pustules, and on one only were they at all comparable in number to those occurring on the apples infected with <i>M. fructigena</i> ; the pustules were ashy grey in colour and the largest was about 0.5 mm. in diameter.
<i>M. fructigena</i> .	Rot had commenced in all, the affected area being 3-13 mm. in diameter.	About half the surface of each was discoloured and all bore yellow (light buff) pustules to 2 mm. in diameter; the pustules were almost localized to a definite circular zone at about 1 cm. from the point of inoculation.

No rot appeared on any of the control apples.

Strong winds, which occurred early in August, detached all the inoculated apples except one. The exception was one infected with *M. fructigena*, which had been in contact with the bark of the branch; the development of numerous pustules served to attach the apple to the

bark, so that although the stalk had become almost severed at the point of its insertion on the fruiting axis, being connected only with a narrow strand of fibrous tissue, the apple still remained *in situ*.

Of the apples found on the ground those inoculated with *M. fructigena* were by this time almost entirely covered with yellow pulverulent pustules, while on those inoculated with *M. cinerea* the pustules were few and small or absent altogether. Most of the apples used as controls were still on the tree.

EXPERIMENT 6.

Monilia fructigena, when growing in stored apples, frequently causes a 'Black Rot' similar in appearance to that produced on those apples artificially inoculated with *M. cinerea* f. *mali*. Spinks (1915), investigating a 'Black Rot' of cider apples, found that 'the apples of the same variety showed the same type of rot irrespective of the fungus with which they were infected', and that 'it seemed certain that the type of rot produced in an apple by *Monilia fructigena* depended only on the apple itself'. An experiment carried out at Wye in 1916 shows that this is not invariably the case, as seen by the results here recorded.

Strains used { *Monilia fructigena*, strain from a plum.
 { *Monilia fructigena*, strain from a 'Black Apple'.

Four apples (variety Bramley's Seedling) were each inoculated on one side with a strain isolated from a pustule of *M. fructigena* growing on a plum, and on the other side with a strain isolated from the fleshy tissue of an apple affected with 'Black Rot'; the inoculations were made on September 8.

RESULT.

	<i>Side inoculated with Plum strain.</i>	<i>Side inoculated with 'Black Apple' strain.</i>
September 13.	A brown discoloration extended from point of inoculation for 2.5-3 cm.; pustules from 60 to 90 in number. The discoloration was a uniform brown, no dark circles at the lenticels.	Discoloration extended 2.5-3 cm. from point of inoculation; the pustules on the four apples numbered respectively 1, 4, 2, and 13. The discoloration was darkest towards centre of affected area, shading off to a brown of the same tint as that on side infected with the plum strain; dark brown circles round lenticels.
September 18.	The whole side was now a uniform brown; no black circles at lenticels; pustules numerous.	Brown colour still darker round point of inoculation; pustules few and scattered; black circles round the lenticels.
October 12.	Pustules numerous, in an almost continuous layer, but showing some tendency to form concentric circles round the centre of infection; the skin, where it could be seen between the pustules, was dark brown to black.	Pustules few and scattered; skin dark brown to black, nigrescence most conspicuous immediately round the lenticels.

Since this experiment pointed to a difference in the physiological reaction of the two strains to the tissues of the apple in which they were growing, the experiment was repeated in 1917 (see Experiment 7) for confirmation of the results, using the same two strains, which in the interval had been cultivated on sterilized media in the laboratory. The results were even more striking than in 1916, showing that the difference was still maintained even after cultivation for twelve months, under similar conditions, as saprophytes.

EXPERIMENT 7.

Strains used—as in Experiment 6.

Two apples were inoculated, as in the previous experiment, on one side with the strain from a plum, and on the other with the 'Black Apple' strain; the inoculations were made on September 14, 1917.

RESULT.

	<i>Side inoculated with Plum strain.</i>	<i>Side inoculated with 'Black Apple' strain.</i>
September 21.	The affected area extended 4-5.5 cm. from point of inoculation; it was bright brown in colour with a rather darker narrow peripheral zone. Numerous yellow pustules, to 2 mm. diam., were present, growing in irregular concentric circles, the first at 1 cm. from the centre.	The rot extended 1-2.3 cm. from the point of inoculation; one apple was of a distinctly darker brown on this side than on the side infected with the plum strain, particularly in a zone 1-2 cm. from the centre, while on the second apple this deeper shade was represented only by two blackish spots at 1 cm. from the centre. No pustules were present, but conidiophores had developed along the wound.
October 12.	The whole of this side was now a bright brown and bore numerous yellow pustules; it was much shrunken and the skin wrinkled.	Skin black and but very slightly wrinkled; no pustules present.

On October 12 the line along which the two strains met was sharply marked, and the black colour of the one side, with its almost smooth skin and absence of pustules, formed a striking contrast to the other (Fig. 7).

By October 25 there was no further change except that the shrinkage was more pronounced, particularly on the side infected with the plum strain.

SUMMARY OF RESULTS OF INOCULATIONS ON APPLES.

Monilia fructigena and *M. cinerea*, when growing on apples, can be distinguished morphologically, the former producing large (up to 2 or even 3 mm. in diameter) yellow pustules, the latter smaller grey ones.

In each species there are two forms which are different physiologically: one which, when growing under the conditions which obtained during the course of the experiments, develops many pustules, and produces a brown

discoloration throughout the affected tissues, and another which develops few or no pustules and causes a discoloration which, primarily brown, gradually becomes darker in the superficial layers until eventually the whole surface is quite black.

Growing apples infected with either species are far more easily detached from the tree than the sound fruit, unless they become attached to the bark, or to other apples in contact with them, by means of the pustules at the point of contact. This fact suggests a reason for the rare occurrence of *M. cinerea* on apples, for the small and comparatively few pustules which it produces appear to be insufficient to attach the fruit to the tree even should infection occur. The writer has occasionally found *M. cinerea* f. *mali* on the very young fruit, but never on any approaching maturity, even on trees severely attacked by the Blossom Wilt disease, while *M. fructigena*, which usually develops numerous large pustules on maturing apples, is extremely common.

Apples, when infected with a form which produces numerous pustules, soon become shrunken and wrinkled, while the skin of those infected with strains which do not develop pustules under those conditions often remains firm and smooth for some time after it has become quite black. The rapid desiccation of the tissues when pustules are present is probably due to two causes: (a) the rupture of the epidermis permitting evaporation from within; (b) loss of water by reason of the respiratory and transpiratory processes in the cells of the hyphae and conidiophores of the pustules.¹

(b) *Plums inoculated with the Two Species.*

These experiments were carried out in two series: (1) inoculations made with the object of comparing the morphology of the two species when growing on plums; (2) inoculations with strains of *Monilia cinerea* for comparing results obtained with the form *mali* with those of the form *pruni*.

The results obtained from inoculating growing plums with a 'Wither Tip' strain of *M. cinerea* have already been published (1918). A similar experiment was made about the same time, i.e. July 1917, using *M. fructigena*; the resulting brown rot was indistinguishable in general appearance from that produced by *M. cinerea*, but the pustules which developed were larger, and yellow in colour. Both species were able to cause infection of uninjured plums in contact with diseased ones by the development of modified pustules at the point of contact, a pad of hyphae being formed which was able to penetrate the skin.

For confirmation of these results, and to obtain a more exact comparison of the two when growing on plums, an experiment was started

¹ When apples bearing numerous *Monilia* pustules are placed in a closed glass vessel, moisture condenses on the internal surface of the vessel within a few hours.

in which inoculations were made simultaneously with the two species on plums in close proximity and also on opposite sides of the same plum.

EXPERIMENT I.

Strains used { *Monilia fructigena*, strain isolated from a plum.
Monilia cinerea, strain isolated from a ‘Wither Tip’ twig of a plum tree.

Plums (variety Victoria) growing in the open were numbered and labelled as follows :

1, 2, and 3 were each a pair of plums at the same node ; one of each pair was inoculated with *M. fructigena*, the other with *M. cinerea*. 4, 5, and 6 were single plums, each inoculated on one side with *M. fructigena*, and on the other side with *M. cinerea*. In the accompanying table the plum or side inoculated with the former is indicated by *f*, and with the latter by *c*.

The inoculations were made on July 17, 1917, by making, in each case, a single puncture through the skin with a sterile needle and placing conidia from a pure culture in the wound.

<i>Six plums, three inoculated with M. fructigena, three with M. cinerea.</i>	<i>No. of mm. through which rot had extended from point of inoculation by July 20.</i>	<i>Result on July 26.</i>			
1 <i>f</i>	5-7	The whole surface was discoloured;	yellow pustules were present;	the fruit-stalk was brown for 3 mm.	
1 <i>c</i>	5-7	„	numerous grey pustules	„ „	4 mm.
2 <i>f</i>	8-9	„	yellow pustules	„ „	3 mm.
2 <i>c</i>	6-8	„	grey „	„ „	12 mm.
3 <i>f</i>	5-8	„	yellow „	„ „	3 mm.
3 <i>c</i>	4-6	„	grey „	„ „	3 mm.
<i>Three plums, each inoculated on one side with M. fructigena, on the other with M. cinerea.</i>					
4 <i>f</i>	9-12 }	The two fungi had met in a plane approximately midway between the two points of inoculation ; <i>M. fructigena</i> had produced fairly numerous yellow pustules, <i>M. cinerea</i> numerous grey ones ; the stalk was brown for 8 mm.			
4 <i>c</i>	6-9 }				
5 <i>f</i>	8-9 }	As in No. 4, but stalk brown for 3 mm.			
5 <i>c</i>	5-7 }				
6 <i>f</i>	9-10 }	As in No. 4, but stalk brown for 12 mm.			
6 <i>c</i>	5-6 }				

The discoloration of the plums was a dull purple brown with both species ; on the whole, the distance from the point of inoculation reached by *M. fructigena* after three days was a little greater than that attained

by *M. cinerea*, the maximum extension for the former being 12 mm. and for the latter 9 mm. The brown colour on the fruit-stalk extended upwards from the point of insertion on the plum, indicating that the disease was advancing from the fruit, along the stalk, towards the branch.

The pustules of *M. fructigena* were to 1.5 mm. in diameter, usually about 1 mm., and their colour was 'Light Buff' of Ridgway's colour charts;¹ those of *M. cinerea* were conspicuously smaller, reaching a maximum diameter of 0.8 mm., the usual diameter being about 0.4 mm., and their colour was 'Smoke Grey' to 'Light Greyish Olive'.

On July 27 plums Nos. 2*f* and 2*c* were removed from the tree and photographed, together with a sound plum from the same tree (Fig. 8); the plum No. 6 was also photographed on the same day (Fig. 9).

The results obtained in this experiment prove conclusively that *M. fructigena* and *M. cinerea* are equally able to cause a 'Brown Rot' of plums, and that under these conditions the two species are morphologically quite distinct, as shown by their fructifications.

EXPERIMENT 2.

The experiment recorded here is one of a series carried out with the object of ascertaining whether the two forms *mali* and *pruni* of *Monilia cinerea* could be distinguished when growing on plums. The experiments were suggested by the fact that of all the strains of *M. cinerea* obtained from plums or cherries (more than 20 in all), not one could be identified, by the characters given later in this paper,² as forma *mali*, and a reason was sought for this absence of the apple form from species of *Prunus*. *M. cinerea* f. *mali* produces pustules less freely on sterilized potato and on apples (as shown in preceding pages) than f. *pruni*, and it was thought that the former, if it did occur occasionally on plums, was unable to become established there, for experiments on apples in the open showed that pustules were necessary for the diseased fruit to be retained on the trees as mummies. Preliminary experiments in the laboratory proved that the form *mali* grows readily when inoculated into picked plums, again with a tendency to develop fewer pustules than does the form *pruni*.

During the summer of 1918 plums growing in the College plantation were inoculated on June 21, June 24, and July 15; on each occasion the strains used were:

M. cinerea forma *mali*, strain from a 'Brown Rot Canker'.

"	"	<i>mali</i> ,	"	"	an apple spur.
"	"	<i>pruni</i> ,	"	"	a mummied plum.
"	"	<i>pruni</i> ,	"	"	a mummied cherry.

¹ Color Standards and Nomenclature. Washington, 1912.

² These features will be discussed in Part II of this paper.

All the strains readily produced on the infected plums the characteristic 'Brown Rot' and numerous pustules. A slight difference could be detected in the productivity of pustules in the two forms in a similar experiment started a little later in the season, viz. Aug. 1, when the fruit was approaching maturity, and the detailed results of this experiment are here tabulated. The pustules are described as 'numerous', 'many', or 'few' in the following sense:

Pustules numerous—occurring scattered over the whole surface and often also becoming confluent to form continuous zones or irregular patches.

Pustules many—scattered over the whole affected surface; continuous patches absent or few and small.

Pustules few—isolated and scattered over a portion (half or less) of the discoloured area.

Two trees (variety Victoria) were reserved for the experiment, ten plums being inoculated on each tree as shown in the table.

The method of inoculation adopted was similar to that used in Expt. 1.

	<i>Strains used in the inocula- tions (Aug. 1).</i>	<i>Plum No.</i>	<i>Aug. 6.</i>	<i>Aug. 13.</i>	<i>Aug. 28.</i>
TREE I.	<i>M. cinerea</i> <i>f. mali.</i> Strain from a 'Brown Rot' Canker on an apple tree.	1	Half the sur- face affected; pustules few.	Whole surface discoloured and wrinkled, plum shrunk; pustules many; two other plums in contact with it were discoloured over their whole surface and bore a few pustules.	The three plums were shrunk and wrinkled and bore many pustules.
		2	Half the sur- face affected; pustules ab- sent.	Whole surface wrinkled, plum shrunk; pustules many; in contact with in- oculated plum were one wholly discoloured and another with $\frac{1}{3}$ of the surface affected, both with a few pustules.	The plum pri- marily inocu- lated had in- fected 4 others; all were shrunk- en and bore many pustules.
		3	The rot had extended 1.5- 2 cm. from point of inocu- lation; pus- tules none.	Whole surface affected; pustules many; another plum, infected from con- tagion, showed a rot ex- tending 1-1.5 cm. from the point of contact.	Both were shrunk and bore many pustules.
		4	The rot had extended 1.3- 1.8 cm.; pus- tules none.	Whole surface affected; pustules many.	Fallen.
		5	Half the sur- face affected; pustules none.	Whole surface affected; pustules few.	Much shrunk and bearing many pustules.

Strains used in the inoculations (Aug. 1).		Plum No.	Aug. 6.	Aug. 13.	Aug. 28.
TREE I.	<i>M. cinerea</i> f. <i>pruni</i> . Strain from a mummied plum.	1	Nearly half the surface affected; pus- tules none.	Whole surface affected; pustules numerous; in con- tact with it were one wholly discoloured with two almost continuous zones of con- fluent pustules, and another with half the surface af- fected and bearing few pustules.	One other had also become in- fected from con- tagion; all four were shrunkened and bore nu- merous very pulverulent pus- tules becoming confluent and forming patches to 5 mm. diam.
		2	Ditto	Whole surface affected; plum shrunkened and wrinkled; pustules nu- merous.	Pustules more numerous; plum still more shrunkened and wrinkled.
		3	One-third of the surface affected; pus- tules none.	Ditto	Pustules more numerous.
		4	Ditto	Ditto	Pustules more numerous; along one side was a long continuous band (3 x 1 cm.) of confluent pustules.
		5	Nearly half the surface affected; pus- tules none.	As above, but with another plum in contact with it also discoloured over the whole surface and bearing many pustules.	Both plums much shrunkened and bearing numerous pus- tules.
TREE II.	<i>M. cinerea</i> f. <i>mali</i> . Strain from a flowering spur of an apple tree.	1	The rot ex- tended 0.5- 1.5 cm. from point of inocu- lation; no pus- tules.	Whole surface discoloured and wrinkled, plum shrunkened; pustules many. Another plum in contact with it was discoloured over half its surface and bore a few pustules.	Both plums shrunkened and bearing many pustules.
		2	Slight dis- coloration only, imme- diately round the wound.	Whole surface discoloured but not wrinkled and plum not shrunkened; pustules none.	Wrinkled and shrunkened; pus- tules few.
		3	Extension of rot 1.0-1.8 cm.; no pus- tules.	Whole surface discoloured, plum a little shrunkened; pustules many.	Wrinkled and shrunkened; pus- tules many.
		4	Extension of rot 1.0-1.5 cm.; no pus- tules.	As in No. 3, but pustules few.	Wrinkled and shrunkened; pus- tules few.
		5	Extension of rot 1.3-1.5 cm.; no pus- tules.	As in No. 3; pustules many.	Wrinkled and shrunkened; pus- tules many.

<i>Strains used in the inoculation. (Aug. 1).</i>		<i>Plum No.</i>	<i>Aug. 6.</i>	<i>Aug. 13.</i>	<i>Aug. 28.</i>
TREE II.	<i>M. cinerea</i> f. <i>pruni</i> . Strain from a mummied cherry.	1	Half the surface affected; no pustules.	Whole surface discoloured and wrinkled, plum shrunk; pustules numerous. One other in contact discoloured over the whole surface but bearing no pustules.	Both plums shrunk and bearing numerous pustules.
		2	One-third of the surface affected; no pustules.	Whole surface discoloured; shrinkage slight; pustules many.	Wrinkled and shrunk; numerous pustules.
		3	Nearly half the surface affected; a few pustules.	As in 2.	As in 2.
		4	Nearly half the surface affected; no pustules.	Whole surface discoloured, plum shrunk; pustules numerous.	Fallen.
		5	One-third of the surface affected; no pustules.	As in 4.	Fallen.

On August 28 some of the plums on these and adjoining trees were ripe; thus those affected from contact with plums artificially inoculated must have become infected just as they were ripening, so that the observations covered the period from the time the plums were quite small (i. e. June 21, when they were not half grown) to their maturescent period. In the experiment started on August 1 (results tabulated) there is evidence that on plums infected near the time of ripening the apple form of *Monilia cinerea* produces fewer pustules than the *Prunus* form; the difference, however, is not striking and both forms readily cause infection of other plums in contact with those primarily infected. The experiments therefore afford no clear explanation of the rare occurrence (perhaps absence) of the form *mali* on naturally infected plums.

The experiment is interesting as illustrating the rapidity with which the rot traverses infected plums. Thus in most cases one-third to one-half the surface was discoloured on the fifth day after inoculation, with the development of pustules in two instances, while on the twelfth day not only were all the primarily inoculated plums affected throughout, but others in contact with these were often also discoloured over their whole surface and bore pustules.

It may here be pointed out that experiments carried out at Wye suggest that in this country plums are infected by the 'Brown Rot' fungi only through wounds. Inoculations made in 1917 by placing conidia of

Monilia fructigena and *M. cinerea* on the uninjured skin of the immature fruit gave negative results. A similar result was obtained in 1918 when conidia of the strain of *M. cinerea* obtained from a plum (the strain used in the experiment just described) were placed on the uninjured skin of 12 young Monarch plums (not half grown) under conditions favourable for their germination, i.e. a gentle rain was falling at the time and the atmosphere was saturated with moisture for at least 12 hours after the inoculations were made. A few days later 12 Victoria plums were similarly treated, and again no infection occurred. Valleau (1915), working in America with the form of *Monilia* which is found there, obtained different results, for he finds 'that infection may take place through the uninjured skin at any time during the development of the plum fruit'.

(c) *Plum Flowers inoculated with Strains of Monilia cinerea.*

During the month of April, 1918, a series of three experiments was carried out on flowers of plum trees in the open, the number of flowers inoculated altogether being 39.

The strains of *Monilia* used in each experiment were :

M. cinerea f. *mali*, strain from a Brown Rot Canker of an apple tree.

„ f. *pruni*, strain from a mummied plum.

„ f. *pruni*, strain from a mummied cherry.

The inclement weather which prevailed during the latter half of April removed many of the inoculated flowers at an early stage in the experiments, but a sufficient number remained long enough for the following conclusions to be drawn.

All three strains were equally able to cause infection of the flowers. Each strain was able not only to kill the inoculated flower but to invade the axis of the inflorescence and so cause the death of all the flowers at that node. In two of the experiments, in which the conidia were placed on the stigmas, the results were similar to those already published (1918) for inoculations carried out in 1917 on plum flowers with a 'Wither Tip' strain of *Monilia cinerea*, except that the progress of the disease, particularly in the early stages, was retarded, this being in all probability due to the lower temperature. The first symptom of infection after inoculation of the stigma is a brown discoloration of the stigma itself, usually within two days ; this is followed by an extension of the browning downwards along the style, which can be followed day by day until the ovary is reached and soon the whole flower is affected.

In the third experiment the conidia were placed inside the flowers so that the disc became inoculated ; in this case the first external evidence of infection was the appearance of a brown patch at one side of the calyx tube. Since the method adopted in making the inoculations and the results

obtained in the early stages of infection in this experiment were different from those of previous experiments the details are given in full.

Small particles of potatoes bearing conidiophores were cut from a pure culture of the fungus growing on sterilized potato and taken to the garden in a sterilized Petri dish, a separate dish being used for each strain. One of the particles was inserted, on the point of a sterilized needle, within the flower in such a way that the conidiophores came in contact with the disc and deposited conidia. The potato particle was then replaced in the dish and another taken for the next flower. Flowers were selected in which there was sufficient space between the stamens and ovary to allow of this operation being carried out without injuring the organs.

The inoculations were made on flowers of Monarch plum trees in the College plantation on April 12; twelve flowers were inoculated, four with each of the three strains.

On April 21 no difference could be detected between the inoculated flowers and others in the vicinity except in the case of one flower (No. 4, inoculated with the cherry strain), the stamens and style of which were withering. Three days later, however, on most of the inoculated flowers there was evidence that infection had occurred.

<i>Strains used in inoculations.</i>	<i>Result, April 24.</i>
<i>M. cinerea</i> f. <i>mali</i> . Strain from a 'Brown Rot' Canker of apple.	<ol style="list-style-type: none"> 1. No discoloration to be detected. 2. Slight browning on inner surface of calyx tube 3. No discoloration. 4. No discoloration.
<i>M. cinerea</i> f. <i>pruni</i> . Strain from plum.	<ol style="list-style-type: none"> 1. Ovary and base of style brown; one side of calyx tube brown on inner and outer surfaces. 2. Inner surface of calyx tube brown on one side. 3. One side of calyx tube brown on both surfaces. 4. No discoloration.
<i>M. cinerea</i> f. <i>pruni</i> . Strain from cherry.	<ol style="list-style-type: none"> 1. Slight discoloration on inner surface of calyx tube. 2. One side of calyx tube brown on both surfaces. 3. Slight discoloration on inner surface of calyx tube. 4. One side of calyx tube brown on both surfaces; style and stamens brown.

When the flowers were next examined, May 7, all had been blown off except two, viz. No. 2 inoculated with the apple strain, and No. 3 with the cherry strain. The former by this time had become withered to the base and the disease had invaded the flowering axis and caused infection of a second flower (also withered) inserted there, while the latter showed a similar result, but in this case both infected flowers bore grey *Monilia* pustules.

The wilting of plum flowers may be produced therefore by inoculation of either the stigmas or the floral disc with conidia of *Monilia cinerea*.

(d) Apple Flowers inoculated with Strains of Monilia cinerea.

In the course of the investigation of the 'Wither Tip' disease of plum trees it was discovered that two morphologically similar strains of *Monilia cinerea* had the power to infect apple flowers in different degrees of intensity. A strain obtained from a diseased plum twig, although it was able to induce withering of the actual flowers inoculated, was unable to proceed beyond the base of these, and the rest of the flowers of the same inflorescence were not affected, while a strain obtained from an apple spur not only readily infected apple flowers but invaded the tissues of the axis of the inflorescence and caused a wilting of all the flowers and leaves borne on that axis (Figs. 10 and 11). These results suggested the occurrence of 'Biologic Forms' within the species *Monilia cinerea*; for confirmation of this conclusion further experiments were carried out in 1918, using other strains of *M. cinerea*.

One of the strains selected had been isolated from a tree of *Pyrus japonica* which was affected with a Blossom Wilt resembling that of the apple. This strain, though obtained from a species of the same genus as the apple, showed certain physiological characters similar to those of strains isolated from species of *Prunus*. It had been isolated from a wilted flower in July, 1917, and when used for inoculations had been cultivated saprophytically on artificially prepared media for ten months. In the experiment in which it was used, a strain obtained from an apple spur in March, 1917, was taken for comparison.

The first experiment of the series was carried out with one strain of the apple form of *Monilia cinerea* originally isolated from a 'Brown Rot' Canker in 1916, but re-isolated in 1917 and again in 1918 from an apple spur which had been infected after artificial inoculation of a flower with a pure culture in 1916. Thus in 1918 the original and two sub-strains were available for the experiment, viz. (1) the original strain which had been growing on artificial media for two years, (2) sub-strain grown for about twelve months artificially, (3) sub-strain isolated a few weeks previous to the inoculations. The experiment was carried out with the object of ascertaining whether the form of *M. cinerea* which causes the Blossom Wilt of apples retains its virulence after continued culture on artificially prepared media.

The strains used in this series of experiments on apple flowers were from various sources and hosts as shown below :

Strain A₁.—Isolated in April 1916 from a 'Brown Rot' Canker of a Cox's Orange Pippin apple tree (specimen sent from Berkshire), and afterwards cultivated in pure cultures in the laboratory.

Strain A₂.—Isolated in March 1917 from an apple spur which had become infected in the College plantation after artificial inoculation in 1916 with a pure culture of Strain A₁.

Strain A₃.—Obtained from the same spur as A₂, but cultures started in March, 1918.

Strain B.—From a naturally infected spur of a Lord Derby apple tree in the College plantation in April, 1918.

Strain C.—From a dead plum twig in the College plantation, isolated March, 1918.

Strain D.—From a mummied plum sent from Cambridgeshire, March, 1918.

Strain E.—From a mummied cherry sent from Mid-Kent, March, 1918.

Strain F.—From a flower of *Pyrus japonica* from Mid-Kent, July, 1917.

The experiments were all carried out on apple trees of the James Grieve variety growing in the plantation. Spurs, each bearing an umbel of several flowers, were labelled and two flowers (*a* and *b*) in each umbel were inoculated. The situation of the inoculated flowers on the spur was noted so that a comparison could be made between inoculated and non-inoculated flowers on each umbel, the latter thus serving as controls during the early stages of infection. The inoculations were made as in the experiment on plum flowers, except that in the present case the conidia-bearing surface of the potato particles was brought in contact with the stigmas.

EXPERIMENT I.

Strains used	A ₁	Apple Blossom Wilt strain, isolated 1916.			
	A ₂	"	"	"	1917.
	A ₃	"	"	"	1918.

The inoculations were made on May 8, 1918, and the results to May 21 are given in the accompanying table :

Strain.	Spur.	Flower.	May 14.	May 18.	May 21.
A ₁	1	a.	Styles brown for 1-8 mm.	All the flowers of the inflorescence dead; leaves at the base of the umbel wilting.	The whole inflorescence, together with leaves at base, was now brown and dead; flowers recurved and leaves curled.
		b.	Stigmas only brown.		
	2	a.	Styles brown to base.	Ditto	Ditto
		b.	Ditto		
	3	a.	Ditto	Both inoculated flowers had brown withered stamens; pedicels brown and wilting; some of the leaves were wilting, but the non-inoculated flowers were upright.	Ditto
		b.	Ditto		

Strain.	Spur.	Flower.	May 14.	May 18.	May 21.
A ₂	1	a.	Styles brown to base.	Brown to base of pedicel ; stamens and calyx lobes brown.	Both flowers dead ; leaves beginning to wilt.
		b.	Ditto	Stamens and calyx lobes brown and withered.	
	2	a.	Ditto	Both flowers brown and withered to the base of pedicels.	Whole inflorescence dead ; flowers brown, withered, and recurved ; leaves brown and curled.
		b.	Ditto		
	3	a.	Ditto	Both flowers brown and withered. The other flowers on this spur and the leaves at base were just beginning to wilt.	Ditto
		b.	Ditto		
A ₃	1	a.	Two styles with brown stigmas only, the others brown to base.	Both flowers had brown withered stamens.	Both flowers brown and withered to base of pedicel.
		b.	All the five styles brown to base.		
	2	a.	Styles brown for 1-4 mm.	Both flowers brown to base of pedicels.	Whole inflorescence dead ; flowers and leaves brown and withered.
		b.	Styles brown to base.		
	3	a.	Two styles with brown stigmas only, the others brown for 1-4 mm.	Both flowers' withered ; stamens and calyx brown.	Ditto
		b.	Styles brown to base.		
	Controls.		Flowers not inocu- lated on these and on other spurs of the same tree had, gener- ally, brown stigmas only, but a few showed a slight browning of the styles also.	The rest of the flowers had brown styles, but the stamens were upright, with white filaments, and the calyx lobes were green and spreading.	On the rest of the tree the flowers at this time were just 'setting' into fruit.

On May 25 the two flowers of spur No. 1 inoculated with strain A₃ had fallen ; the spur itself was not affected and one of the non-inoculated flowers was 'setting' into fruit. The fungus had by this time advanced some distance into the tissues of the other infected spurs, as distinctly shown in those cases where the spur was branched and bore two inflorescences, one of which bore inoculated flowers ; the non-inoculated umbel and the accompanying leaves were withered, thus indicating that the transpiration current had been interrupted at its junction with the main axis of the spur, which therefore must have been invaded by the fungus

travelling downwards from the other (infected) umbel. To bring about this result the fungus must have traversed a distance of from 4.5 to 5.5 cm. between the time of inoculation, on May 8, and May 25.

This experiment proves conclusively that the virulence of the apple Blossom Wilt form of *Monilia cinerea* is not diminished after from one to two years' culture as a saprophyte on artificially prepared media in the laboratory. It also shows that the conidia produced on a spur during the second year after infection occurs are as virulent as those produced during the first year subsequent to infection.

EXPERIMENT 2.

Strains used	{	B. Apple Blossom Wilt strain, isolated 1918.
		C. A 'Wither Tip' strain from a plum tree, isolated 1918.
		D. From a mummied plum, isolated 1918.
		E. „ „ cherry, „ „

The inoculations were made on May 9, 1918.

It will be seen from the table that during the first six days after inoculation the symptoms of infection were generally similar for all the four strains; later the apple Blossom Wilt strain made rapid progress and caused, in the case of two spurs, the death of the whole inflorescence and the leaves borne on the spur, while with the other strains the disease was confined to the flowers actually inoculated, i. e. the tissues of the spurs were not invaded and the leaves were unaffected.

On May 15 a comparison of the inoculated and the non-inoculated flowers showed that in the former infection had occurred in every case; this, together with the fact that of the eighteen flowers inoculated with strains C, D, and E all had fallen except two, leads to the conclusion that these strains either kill the flowers directly or at least infect the styles and so prevent pollination, the final result being the same, viz. the arrest of any further development of the flowers, which in consequence wither and fall off. The one instance in which the ovary did begin to swell probably means that pollination had occurred in that case before the inoculation was made.

Strain.	Spur.	May 15.			May 19.		May 22.		May 28.	
		a.	b.		Both flowers brown and withered to base of pedicel; calyx lobes withered.	Withered to base of pedicel. Stamens and calyx brown and withered.	All the flowers and leaves on the spur brown and withered.	Flower dead. Fallen.	Cortex brown to base of spur, i.e. for 5 cm. from the insertion of the flowers; a vegetative shoot on same spur dead.	
B.	1	Styles brown to base.								
		Ditto								
	2	a. Styles brown for 3-6 mm.	b. " " 4-6 mm.							
C.	3	a. Styles brown for 6-10 mm.	b. " " 1-2 mm.							
	1	a. Styles brown for 2-10 mm.	b. " " to base.							
	2	a. Styles brown to base.	b. Ditto							
D.	3	a. Ditto	b. Ditto							
	1	a. Styles brown for 3-4 mm.	b. " " 8-10 mm.							
	2	a. " " 3-6 mm.	b. " " 3-5 mm.							
	3	a. " " 3-5 mm.	b. " " 3-8 mm.							

Both flowers brown and withered to base of pedicel; calyx lobes withered.

Withered to base of pedicel. Stamens and calyx brown and withered.

Withered to base of pedicel. Stamens and calyx brown and withered.

Styles brown to base.

Half the stamens and two calyx lobes brown.

Stamens brown.

Stamens and calyx lobes brown.

Half the stamens brown.

Stamens and calyx lobes brown.

Indistinguishable from controls.

Stamens wilting.

Indistinguishable from controls.

Ditto

Stamens and calyx brown, also 0.5 cm. of pedicel.

Indistinguishable from controls.

Cortex brown to base of spur, i.e. for 5 cm. from the insertion of the flowers; a vegetative shoot on same spur dead.

Both fallen.

All flowers and leaves on the spur dead; a vegetative shoot on the same spur wilting.

Both flowers fallen; two others of the same umbel are alive and the leaves show no signs of wilting.

All the flowers fallen; leaves healthy.

Both flowers fallen; one other flower on the same spur had developed into a fruit 1 cm. in length; leaves healthy.

Both dead; one other flower on same umbel alive; leaves healthy.

Flower dead.

Developing into fruit.

All flowers of the umbel fallen; leaves healthy.

As on May 19.

Pedicel brown for 1 cm. below ovary.

EXPERIMENT 2 (*continued*).

Strain. E.	Spur.	May 15.		May 19.		May 22.		May 28.	
		a.	b.	Styles brown to base; stamens beginning to wilt; calyx lobes brown at tip.	Both indistinguishable from controls.	Stamens brown and collapsed.	Indistinguishable from controls.	Both flowers fallen; two others on same spur forming fruit; leaves healthy.	a. Flower alive but ovary not swollen. b. Flower dead.
	1	a. Styles brown for 5-10 mm.	b. " " 1-5 mm.						
	2	a. " " 1-6 mm.	b. " " 3-10 mm.						
	3	a. " " 8-10 mm.	b. " " to base.	Ditto		a. Flower withered to base of pedicel. b. Indistinguishable from controls.		Both flowers fallen; one other flower on the same spur had developed into a fruit 1 cm. long; leaves healthy.	
	Controls.	Flowers not inoculated generally with brown stigmas only; a few showed a slight discoloration of the style.		Styles brown to base, but stamens upright with white filaments; calyx lobes green and spreading.		Controls generally with upright stamens and white filaments, tips of calyx lobes brown; a few flowers had set into fruit—these have brown stamens.		Healthy flowers and mostly developed into fruit up to 1 cm. in length.	

EXPERIMENT 3.

Strains used { A₂. Apple Blossom Wilt strain, isolated 1917.
F. Strain from *Pyrus japonica*, isolated 1917.

The inoculations were made on May 11, 1918.

Strain.	Spur.	May 17.	May 21.	May 24.	May 30.
A.	1	a. Styles brown for 9-10 mm. b. " " to base.	Styles of both brown to base, but stamens upright and calyx lobes green and spreading as in controls.	Both flowers fallen; one other flower on the spur developing into fruit.	Fruit of developing non-inoculated flower now 1 cm. in length.
	2	a. " " b. " "	Both flowers withered to base of pedicels; stamens brown and collapsed; the rest of the flowers on this spur also dead and leaves wilting.	All the flowers of the spur withered on brown recurved pedicels; all the leaves brown, withered, and curled.	Cortex of spur brown and dead for 3 cm. below the insertion of the flowers.
F.	1	a. " " b. " "	Both flowers brown and withered to base of pedicels; the other flowers on the spur alive and healthy.	Both inoculated flowers fallen.	Fruit of a non-inoculated flower on this spur 1 cm. in length.
	2	a. " " b. " "	Styles brown to base in both; filaments of stamens upright.	a. Stamens brown and withered. b. Stamens wilting.	a. Withered to base of pedicel. b. Fallen.
	3	a. " " b. Two styles with brown stigmas only. Three styles brown for 2-5 mm.	Styles brown to base in both; stamens and calyx as in controls.	a. Stamens brown and withered. b. Stamens and calyx lobes brown and withered.	a. Withered to base of pedicel. b. Fallen.
	4	a. Styles brown for 7-10 mm. b. " " 6-10 mm.	As in controls.	Stamens brown and withered in both; one other flower on same spur developing into fruit.	a. Dead } One non-inoculated flower forming fruit b. Fallen } 1 cm. in length.
Controls.		Flowers not inoculated show generally no discoloration at all or a browning of the stigmas only, but in a few instances styles were brown for 1 mm.	Styles usually brown to base; stamens upright with white filaments; calyx lobes green and spreading.	Generally with stamens withering, but many still with white filaments; some flowers developing into fruit (ovary swelling).	Controls, in those cases where the fruit has 'set', have fruit about 1 cm. in length.

As in Expt. 2 the brown discoloration of the styles of all the inoculated flowers on the sixth day after the commencement of the experiment showed that infection had taken place. All these flowers failed to develop into fruit; in the case of one of the spurs infected with the apple strain the typical Blossom Wilt condition was produced, the whole inflorescence together with the leaves on the spur becoming withered within ten days. In this experiment the strain from *Pyrus japonica* proved to be less virulent than the apple Blossom Wilt strain, and is therefore more nearly allied, biologically, to the form of *Monilia cinerea* found on plums and cherries.

EXPERIMENT 4.

Strains used { C. A 'Wither Tip' strain from a plum tree.
 D. From a mummied plum.
 E. " " cherry.

The inoculations were made on May 11. This experiment was made to supplement Expt. 2, the three strains being the three *Prunus* strains used on that occasion.

Strain.	Spur.	May 17.	May 21.	May 24.	May 30.
C.	1	a. Styles brown to base. b. Ditto	Not distinguishable from controls.	Both fallen.	No fruit developing from any of the flowers, but spur alive and leaves healthy.
	2	a. Ditto b. Ditto	Ditto	a. Fallen. b. Developing into fruit.	b. Fruit 1 cm. long.
D.	1	a. Styles brown for 2-5 mm. b. One style brown for 6 mm., the other four have brown stigmas only.	Not distinguishable from controls.	a. Stamens turning brown. b. Fallen.	Both inoculated flowers fallen one other has developed into fruit 1 cm. long.
	2	a. Styles brown for 4-7 mm. b. " " 2-3 mm.	Ditto	a. Fallen. b. Fallen.	All the flowers on this spur fallen, but leaves healthy.
E.	1	a. " " 3-10 mm. to base. b. " " "	Both flowers brown and withered to base of pedicels.	No further change noticeable.	All the flowers fallen, but leaves healthy.
	2	a. " " " " b. " " for 5-7 mm.	a. Ovary brown; stamens brown and collapsed; calyx lobes withering. b. Styles brown to base.	Both fallen.	Two non-inoculated flowers have formed fruit 1.5 cm. long.
Control.		Flowers not inoculated generally show no discoloration or a browning of stigmas only; occasionally a style is brown for 1 mm.	Styles mostly brown to base; stamens not yet withered; calyx lobes green.	Most flowers with withered stamens, but many have still white upright filaments.	In those flowers where the fruit is 'setting', it is about 1 cm. in length.

Again observations on the sixth day after inoculation showed that infection of the styles had occurred. As before, one inoculated flower developed into fruit; the rest all became withered and fell off.

The results of these four experiments, together with those obtained in the experiment carried out in 1917, may be summarized as follows:

RESULTS OF INOCULATIONS MADE ON APPLE FLOWERS WITH
STRAINS OF *MONILIA CINEREA*.

				No. of flowers inoculated.	No. of spurs on which the in- oculated flowers were situated.	No. of spurs killed.	No. of inoculated flowers which developed into fruit.
' Blossom Wilt and Canker' strains of <i>Monilia</i> <i>cinerea</i> from ap- ple trees	1918	A ₁		6	3	3	0
		A ₂		10	5	4	0
		A ₃		6	3	2	0
		B		6	3	2	1
	1917	A ₂		4	4	4	0
Total . .				32	18	15	1
Other strains of <i>M. cinerea</i> from various sources	1918	Plum		10	5	0	1
		Cherry		10	5	0	0
		' Wither Tip' of plum		10	5	0	1
		<i>Pyrus</i> <i>japonica</i>		8	4	0	0
	1917	' Wither Tip' of plum		10	4	0	0
		Total . .		48	23	0	2

Thus of the 18 spurs bearing flowers which had been inoculated with the strains from apple trees, 15 were killed outright, with all their flowers and leaves, while the inoculation of 48 flowers with strains from sources other than the apple did not produce in any one instance infection of the tissues of the spur, although there was evidence that infection of the flowers actually inoculated had occurred.

The conclusion is, that the 'Blossom Wilt and Canker Disease' of apple trees is caused by a specialized form of *Monilia cinerea*.

Woronin (1900) stated, as a result of his own inoculation experiments on apple flowers, that *M. cinerea* was unable to produce a Blossom Wilt of apple trees. The host from which he obtained the strain used in his experiments is not stated, but in all probability it was a cherry or plum; had he worked with a strain taken from a dead spur or canker of an apple tree he might have obtained a different result.

VI. CONCLUSIONS.

A general discussion of the results recorded in the present article is reserved for a future occasion, when they will be correlated with those of

certain physiological and cultural experiments carried out with the same fungi. It will be convenient, however, to summarize briefly the results of the observations and experiments described in the preceding pages, as follows:

1. In this country two distinct species of *Monilia* occur as parasites on fruit trees, viz. *M. fructigena*, Pers., and *M. cinerea*, Bon.

2. Each species has two forms distinguished by the effects produced on mature apples inoculated under laboratory conditions.

3. The morphological species *Monilia cinerea* includes two 'biologic' forms, one of which produces a 'Blossom Wilt and Canker Disease' of apple trees, and another which is unable to cause infection of the apple inflorescence other than the flower actually inoculated.

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EXPLANATION OF PLATES XXV AND XXVI.

Illustrating Mr. Wormald's paper on the 'Brown Rot' Diseases of Fruit Trees.

PLATE XXV.

- Fig. 1. Plums naturally infected, above with *Monilia cinerea*, the two below with *M. fructigena*.
 Fig. 2. Plums naturally infected, the one on the right with *M. fructigena*, the one on the left with both *M. fructigena* (right side) and *M. cinerea* (left side).
 Fig. 3. Fruiting spur of apple bearing pustules of *M. fructigena* in late summer; infection occurred through the fruit, the stalk of which is seen at the upper end.
 Fig. 4. Apple (var. Bramley's Seedling) inoculated with pure cultures, on the left with *M. fructigena*, on the right with *M. cinerea* f. *mali*: result on seventh day after inoculation. At this stage the dark rings round the lenticels on the side infected with *M. cinerea* f. *mali* are a characteristic feature.
 Fig. 5. The apple shown in Fig. 4, but 13 days later; the right side of the apple was quite black by this time.
 Fig. 6. Apple inoculated from pure cultures, on the right with *M. cinerea* f. *mali*, on the left with *M. cinerea* f. *pruni*.
 Fig. 7. Apple inoculated from pure cultures with two strains of *M. fructigena*, on the left a strain from a plum, on the right a strain from an apple affected with 'Black Rot'.
 Fig. 8. On the left a plum inoculated from a pure culture of *M. fructigena*, on the right a plum inoculated from a pure culture of *M. cinerea*. Control plum, from the same tree, in the centre.
 Fig. 9. Plum inoculated from pure cultures, on the left with *M. fructigena*, on the right with *M. cinerea*. (The experiments illustrated by Figs. 8 and 9 were carried out in the open, the specimens being removed from the tree immediately before the photographs were taken.)

PLATE XXVI.

- Fig. 10. Above, on the left, an inflorescence of an apple tree (var. Lord Derby), of which a single flower had been inoculated with conidia from a pure culture of *M. cinerea* f. *mali*; infection has reached the base of the spur and a canker is just making its appearance on the stem. Result 16 days after inoculation.

Fig. 11. As in Fig. 10, but 5 days later ; the canker has nearly girdled the stem.

Fig. 12. A canker, from an apple tree infected with *M. cinerea* f. *mali*, bearing pustules during the third year after infection ; photographed in January, 1919. (The same canker photographed in 1917, one year after infection, is shown in the Jour. Bd. Agric., Aug., 1917, p. 504, Fig. 1.)

Fig. 13. Dead spur and canker from an apple tree (var. Warner's King) photographed Mar. 22, 1918 : result of inoculating a single flower of the inflorescence in May, 1916, with conidia from a pure culture of *M. cinerea* f. *mali*. The canker produced in 1916 is nearly covered by callus, but the spur still bears pustules of viable conidia.

Fig. 14. Dead spur and canker of an apple tree (var. James Grieve), winter condition, the result of the natural infection of the fruit with *M. fructigena* during the previous summer : the fruit-stalks, from which the diseased apples had fallen, are seen at the apex of the spur. The fungus was isolated from barren pustules on the spur and from mycelium in the canker. (Compare Fig. 3, which shows the summer condition of the fungus on an apple spur.)

Fig. 15. Above are two flowering spurs which had become infected by *M. cinerea* f. *mali*, resulting in a canker on the branch. The check to the upward flow of sap stimulated buds below the canker to grow out into weak vegetative shoots.

Fig. 16. Section through an infected spur and canker of an apple tree. The lesion on the branch is being covered by callus. $\times 2$.

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