Croonian Lecture.—"On some Relations between Host and Parasite in certain Epidemic Diseases of Plants." By H. Marshall Ward, F.R.S., Professor of Botany, Royal Indian Engineering College, Cooper's Hill. Received and read February 27, 1890.

Introduction—Relations between Physiology and Pathology.

I thought I could not better respond to the honour of the invitation to give the Croonian Lecture this year than by choosing a subject from the domain of plant pathology, which should, at least, have the merit of being of general interest and importance, and it seemed probable that an account of some of the more conspicuous features and recent results of the study of certain fungoid diseases might be so placed before you that it should illustrate not only the kind of progress which plant pathology is making, but also show how dependent that progress is, and must be, on the advances of physiology. Moreover, I hope to be able to demonstrate that the connexion between these two modern branches of science is (in botany, at any rate, and I have no reason to doubt that the truth applies to the animal kingdom as well) so close and so mutual that the problems which arise daily appeal to students of both departments, and necessitate that each shall know what the other is about. This, of course, is not the same as saying that either branch of study is deficient in its special questions; but it cannot be too much insisted upon that, while the facts and generalisations of pathology often throw light on physiological questions, the enquirer into the pathology of plants has to pause at almost every step and ask some question in physiology, and his progress may be slower or more rapid in proportion as the answer is obscure or the reverse.

For, after all, the pathology of plants embraces those phenomena of abnormal life-processes which can go on in the long series of changes between normal, healthy, vigorous life, and the cessation of that life as such, *i.e.*, death; and it is obviously impossible to study these abnormal life-processes (pathological) without reference to the normal ones (physiological). In other words, then, pathology is the study of disturbed or abnormal physiological processes, and I thought that it would be possible to interest you in some of the phenomena of abnormal plant life, and especially in the working of some of these factors which result in producing certain diseases, in which fungi play the prominent part, and which occasionally assume the nature of epidemics so suddenly that the phenomena continually prove too much for the inherent credulity of those who are not in the habit of

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investigating complex chains of causation, and give rise to speculations of the most superstitious description.

The Diseases of Plants and their Classification, &c.

The diseases of plants have been classified in various ways, at different times, and by different observers. Passing over the earlier attempts,* based for the most part on errors which were natural at

FIG. 1. A young coffee plant (reduced), the leaves of which are badly infected with the Uredinous fungus *Hemileia vastatrix*. The paler spots are bright orange-yellow, the centre gradually turns brown, and then black as the tissues are destroyed; the granular appearance on the younger spots is due to the spores of the fungus. Such yellowing of the leaves is a common symptom of such diseases.

* An excellent account of the earlier writers appeared in the 'Gardener's Chronicle,' 1854, from the pen of the late Rev. M. J. Berkeley, F.R.S.

the time, but some of which seem almost incomprehensible now, as some of our present errors will appear in the future, it may be said that no very exhaustive survey of these diseases as a whole was possible until comparatively recent times. The successive attempts of modern authors* have been almost entirely along one or other of two lines: they have classified the diseases either (1) according to the symptoms externally visible and the organs attacked, or (2) according to the causes which seem most concerned in producing the disease.

Whichever method is adopted, it is repeatedly found that large assumptions have to be made and recognised in order to bring given diseases into the sphere of treatment for the time being, and difficulties of very peculiar nature continually make themselves felt.

As an instance, we may take the well-known symptom of the appearance of yellow leaves. Not only are yellow leaves characteristic of many diseases due to fungi of the groups Uredineæ and Ascomycetes (*Peziza*, *Hysterium*, *Polystigma*, *&c.*), or to the attacks of insects (*e.g.*, Aphides), but they may indicate "something wrong" at the roots—want of drainage, over-drainage, or lack of some ingredient such as iron, or the presence of some noxious mineral, to say nothing of parasites (*Phylloxera*, *Melolontha*, *Agaricus melleus*, *&c.*).

In cold weather in the spring yellow leaves may mean that the temperature is too low for the production of the green chlorophyll; while frost is responsible for the yellowing of other leaves by a totally different procedure—the acid substances in the cells are enabled to diffuse through to the chlorophyll corpuscles and kill them.

Yellow leaves often indicate the access of too little sunlight, but they may be produced by too intense insolation and consequent destructive changes in the cells.

Leaves injured by acid gases and poisonous substances in smoke also turn yellow, and the yellow hue of autumnal leaves is well known, while we have numerous yellow varieties of leaves among cultivated plants, the causes for which are less clear.

These are by no means all the cases observable, but they will suffice to show how little can be inferred from a symptom which may be due to so many causes, operating alone or in combination, be it said. In fact, as a symptom, the yellowing of leaves is of scarcely any classificatory value, and we are driven to the conclusion that the leaves of plants react to most injuries by turning yellow.

It is much the same with other classes of disease named after the prominent symptoms. What is usually termed "canker," for

* The literature is for the most part in Hallier's 'Phytopathologie' (1868), Frank's 'Krankheiten der Pflanzen' (1880), and Sorauer's 'Pflanzenkrankheiten' (2nd ed., 1886).

FIG. 2. Oaks in the neighbourhood of a manufacturing town, the leaves of which were damaged by acid gases. The injury results in the production of yellow spots on the leaves, and the latter eventually turn wholly yellow and brown, and die. From a photograph taken August 8th, 1882.

instance, is in different cases referred by different authorities to the agency of excessively low temperature (frost*), or of insects,† or of fungi,‡ or of two of these combined, to say nothing of other causes. If we now ask how the matter stands with regard to the method of classifying diseases of plants according to their chief causes, the answers are no clearer. It is the custom to proceed somewhat as follows:—

There are, *first*, diseases due to the action of the non-living environment (soil, climate, mechanical injuries, &c.); and, *secondly*, diseases due to the attacks of living beings (parasitic insects, fungi, &c.).

Now, leaving out of account altogether certain totally unexplained diseases, such as some forms of "gumming," &c., it becomes apparent that we are liable to all kinds of errors unless we recognise that no one factor ever accounts for a disease; it is not so obvious, however, that the changes which result in disease are usually due to several factors acting in concert or successively, and I shall try to show that, even in marked cases, it is by no means always easy to decide which

* Sorauer 'Pflanzenkrankheiten' vol. 1, 1886, pp. 305—448.

† Frank, 'Krankheiten d. Pflanzen,' 1880, p. 719.

‡ Hartig, 'Lehrb. d. Baumkrankheiten,' pp. 89 and 109.

FIG. 3. The same oaks as those of fig. 2, photographed from the same spot on July 20th, 1888. The cumulative injury to the leaves in successive years results in the death of the trees.

of the co-operating factors are to be brought into the foreground, though, until this is decided, it may be a hopeless task to consider prophylactic measures. As examples of the complex interactions that may be met with in the first group of diseases as arranged above, we might consider the following :—

A soil is said to be unsuitable as regards aspect, or elevation, or steepness, but it will be evident that the degree of unsuitableness may vary with the depth and structure of the soil, and with the latitude, the proximity of mountain ranges or the sea, and other factors which influence the climate ; instances of disease, in the broad sense of the word, are frequent enough where two neighbouring crops or growths of the same species of plant suffer in very different degrees, owing to slightly different combinations of such factors of the environment; and the difficulty of referring the disease more especially to any one cause only increases with experience. Or, take the structure, &c., of the soil. It may vary in chemical composition, in capacity for retaining water, in physical texture, and so forth; and the enormous differences to be met with are best known to those who have to cultivate large estates or continuously observe large tracts of country. But it is matter of general experience that the chemical composition of a soil is one of its least important features

within wide limits; much more important is the amount of water and air in it, and the way they are held there. These, especially under certain crops, affect the climate of the immediate locality, and all kinds of complexities result. To mention one only, there are certain combinations of soil and climate, &c., which result in the trees being "frost-bitten" whenever there are late spring frosts. In some cases it is found that mere drainage puts an end to the evil; this means not only a removal of water, but an increase of air in the soil and general elevation of temperature. In others it is noticed that the more shaded trees suffer most; this is in part because their tissues are more watery, and their cell-walls more delicate. In others the injury occurs on a particular side of the tree, and is ruled chiefly by the prevailing winds. Now, here is a problem of considerable complexity. Frost (*i.e.*, too low a temperature) is the agent directly concerned, but it accomplishes the injury because the shoots are too succulent, and the tissues too feebly developed, to resist a temperature which they would be perfectly able to resist if more carbohydrates had been formed under a brighter light, and if less water containing more oxygen had ascended their stems, and so forth.

It is at least difficult to class such cases, and they arise every day. Who would have suspected that one result of bringing the larch down from its mountain home would be to render it more liable to injury from certain pests kept in abeyance on its native Alps, because it is stimulated to put forth its young leaves when the insects are about, which puncture the cortex and afford means of entrance for certain parasitic fungi?

On turning attention to the diseases referred to the action of living organisms, we meet with difficulties rather greater than less, and it is chiefly on account of these that so many wild hypotheses are current as to this class of diseases.

Omitting more than a mere reference to the diseased or weakened conditions due to competition with weeds, and with overbearing associates, such as *Thelephora laciniata*, which may overshadow young Conifers, and eventually kill them simply by depriving them of light,* and to the various parasitic Phanerogams such as *Loranthus*, the mistleto, dodder, &c.,† we come to an enormous series of diseases due to parasitic insects (and other animals) and fungi.

The chief difficulty connected with the investigation of diseases induced by fungi is due to the double set of complications involved. It is difficult enough to unravel the tangled skeins of causes and effects

* R. Hartig in 'Untersuchungen aus d. Forstbot. Institut zu München,' 1880, p. 164.

† See Solms-Laubach, "Ueber den Bau und die Entwicklung der Ernährungs-organe paras. Phaner." ('Pringsheim's Jahrbücher,' vol. 6, 1867–8, p. 509).

in the case of the comparatively simple diseases referred to above; but when the problem consists in disclosing the life-history of a microscopic fungus on the one hand, and then in discovering its relations to the plant (the biology of which is always assumed to be known) on or in which it passes the whole or part of this life-history, on the other, the matter rapidly attains unexpected proportions. Yet this is never the whole, or necessarily the major part, of the *real* problem—the nature of the disease—and before that can be even approximately solved we have to obtain an insight into the influence of the non-living environment on both the host-plant and the parasitic fungus, an inquiry which may assume appalling proportions before it is far advanced.

Nor is this the end, though it is quite sufficient to account for the fact that we never know all about any of these diseases.

There is a factor—or set of factors—which always tends to baffle the inquirer into these matters, and that is the internal disposition* of the parts of the organisms concerned; call it what we will—constitution, inherited disposition, &c.—the fact remains that the host-plant and the parasite alike exhibit peculiarities of behaviour that cannot be explained in the present condition of science as directly due to the action of any external agency of the environment, although we are no doubt right in concluding that it is the outcome of the cumulative results of the vicissitudes of the species and its ancestors in the long past.

But it is just the reactions of this constitution, and its variations induced by changes in the physical environment, which are so often and so persistently overlooked, although the attempt to understand any disease is hopeless, unless we take them into consideration. I hope to show, in the course of this lecture, how the modern study of the pathology of plants differs in methods from that of our predecessors, especially in this very particular—the recognition of the reactions of the host to its living and non-living environment, as apposed to the reactions of the parasite to *its* living and non-living environment, and, further, of the truth that disease is the outcome of a want of balance in the struggle for existence just as truly as normal life is the result of a different poising of the factors of existence.

Of course, inasmuch as the abnormal state of affairs, while detrimental to the host, is the best possible for the parasite, we have here the elements of a paradox; but there is no real confusion of ideas here; we are concerned with a particular case, illustrative of the struggle for existence, in which a given set of variable factors of the environment favour one organism at a time when they disfavour another.

* Sachs, 'Lectures on the Physiology of Plants,' pp. 189—204.

The Host-plant, and the Behaviour of its Normal Tissues.

I begin by briefly calling attention to the healthy tissues of a normal green flowering plant, and we need only consider for the moment what is going on in the parenchyma cells of a leaf or stem, such as every one knows the anatomy of. In a selected piece of such tissue we find the mass cut up into a number of thin-walled chambers, the cells, each of which contains a lining of living, colourless protoplasm, with strands or plates of the same running across; in this protoplasm are embedded the nucleus and the green chlorophyll

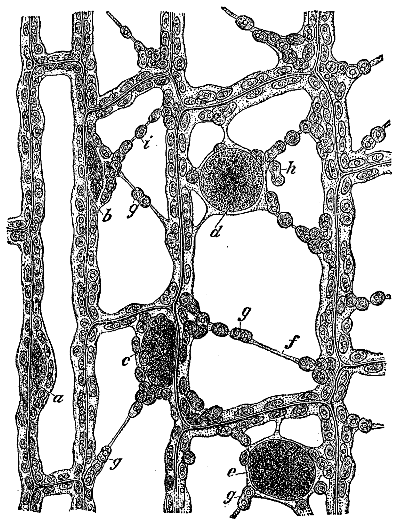

FIG. 4. Portion of the cell-tissue of a higher plant, in longitudinal section and highly magnified. Each of the cells is bounded by the cellulose cell-wall; and this is lined by the protoplasm in which are embedded the nucleus (*a*—*e*) and the green chlorophyll corpuscles (*g*—*i*). This protoplasm encloses the cell-sap, and strands of the former may pass across (as at *f*), or plates of protoplasm may separate the sap of one part of the cell from that of another (Kny).

corpuscles. In the large vacuoles or sap-cavity of each cell is a clear liquid, the cell-sap, consisting of water with small quantities of mineral salts, dissolved gases, organic acids, and salts and other crystalline and non-crystalline substances in various proportions at different times.* Of course, I need not here enter into a long de-

* On the subject of the extreme complexity of the cell-sap and protoplasm, see Pfeffer, "Beiträge zur Kenntniss der Oxydationsvorgänge in lebenden Zellen" 'Abhandl. Math.-phys. Classe Sächsischen Gesellsch. d. Wiss.,' vol. 15, 1889, pp. 455—466).

scription of the histological peculiarities of the cell, and it will probably suffice to remind you that great differences occur in detail as to the size of the cell, the thickness of the wall, number and sizes of the chlorophyll corpuscles, and the presence or absence of colouring matters, crystals, various organised bodies, and so forth. Finally, it will be remembered that all the parts—cell wall, nucleus, chlorophyll corpuscles, and protoplasm generally*—are more or less thoroughly saturated with water, and that aqueous vapour and gases will be found in varying proportions in the passages between the cells, and continuous with the atmosphere, on the one hand, and with the water in the roots and soil, on the other.

Let us now inquire what these normal living cells are doing when they still form an integral part of the tissues of the healthy plant.

In the first place, they are respiring. That is to say, the protoplasm absorbs oxygen gas† brought to it in the water from the roots, from the intercellular spaces which communicate with the atmosphere by means of stomata and lenticels, and from the chlorophyll corpuscles when they are assimilating in bright light. This oxygen enters in solution into the protoplasm, and combines with some of the bodies which for the time being enter into the composition of this complicated structure. The effects of these unions of the oxygen are expressed in molecular disturbances in the protoplasm: some bodies are broken down, others enter into new unions. Finally, the disturbing actions of the energetic oxygen result in the combustion of certain carbon-compounds to carbon dioxide and water, and these escape from the field of action: such combustion implies the liberation of energy, and we recognise this in the complicated movements and life-processes set up in the protoplasm and in the rise of temperature, which can be proved to take place.‡ One point of importance should be insisted on from the first. When the oxygen-molecule enters the protoplasm, it must be pictured as coming into a busy arena, where numerous but definite possibilities are presented to it, and although we are not in a position to trace its movements,§ and the intermediate effects of these, in detail, the evidence shows that while the quantities produced accord with the general view that it is such substances as glucose,

* For particulars as to these, *cf.*, *e.g.*, Zimmermann, "Die Morph. und Physiol. der Pflanzenzelle;" Schenk's 'Handbuch,' vol. 3, Heft 2, pp. 497—700; and Noll, "Die wichtigsten Ergebnisse der botanischen Zellenforschung in den letzten 15 Jahren" ('Flora,' 1889, pp. 155—168).

† *Cf.* Sachs, 'Lectures on the Physiology of Plants,' pp. 395—408; Vines, 'Physiology of Plants,' pp. 195—202; Pfeffer, 'Pflanzenphysiologie,' vol. 1, pp. 346—363.

‡ Rodewald, 'Pringsheim, Jahrb. f. wiss. Bot.,' vol. 17, 1886, p. 338; vol. 19, 1888, p. 221.

§ It may be regarded as certain that for respiration it does not suffice for a body to be merely in the protoplasm (see Pfeffer, 'Oxydationsvorgänge,' pp. 489—490).

and similar carbohydrates, which yield the fuel and energy—as they do in ordinary combustion—nevertheless, we must not fall into the error of supposing that so much sugar or starch in the protoplasm is forthwith and simply oxidised to carbon dioxide and water, nor may we conclude that the process is one of simple and direct oxidation at all.*

In the first instance, it is chiefly owing to the vagaries of the oxygen-molecules in the living protoplasm, that the latter exercises the processes of *metabolism*, the second group of functions we have to consider.

The metabolic processes which can be referred to the changes brought about during respiration† result in two series of events. On the one hand, compounds of various kinds pass out of the protoplasm —the arena of metabolic activity—into other parts of the cell, and especially into the cell-sap; and, on the other hand, bodies of comparatively simple constitution are brought from the cell-sap and elsewhere into the arena of activity, and there worked up into more complex bodies. It is impossible to separate these two sets of processes; but, if we abstract them mentally, for purposes of simplicity, we may say that the following series of events important for our present purposes are taking place.

Carbohydrates, especially in the form of glucoses, are being taken up into the protoplasm, and built up into the structure of its substance: here, owing to the attacks of the oxygen of respiration, the structures into which they enter are more or less broken down—as before said, not necessarily merely oxidised as such or directly—and the complex into which they have temporarily entered becomes decomposed, again to be built up anew by the aid of more carbohydrates, and so on repeatedly.

Among the temporary products of these *destructive* processes, in the complex alternations of building up and breaking down here going on, we find certain nitrogenous compounds (amides and allied bodies) like asparagin, leucin, glutamin, &c., playing important parts. The evidence goes to show that so long as plenty of carbohydrates are at the disposal of the protoplasm, these amide-bodies are again worked

* For the older literature, see Pfeffer, 'Pflanzenphysiologie,' vol. 1, p. 353; Sachs, 'Lectures on the Physiology of Plants,' pp. 395—408: and Vines, *op. cit.*, p. 214. Then consult Palladin, in 'Berichte d. Deutsch. Botan. Gesellsch.,' 1886, p. 322; 1887, p. 325; 'Botan. Centralblatt,' vol. 33, 1888, p. 102; Pfeffer, "Beiträge zur Kenntniss der Oxydationsvorgänge in lebenden Zellen" ('Abhandlg. Math.-phys. Classe Sächsischen Gesellsch. d. Wiss.,' vol. 15, No. 5, 1889, pp. 375—518, especially 480—500), where the more important special literature is quoted.

† Strictly speaking, metabolism includes all the chemical changes in the protoplasm which constitute it living substance; it is a mere convention to speak of different kinds of metabolism, and to separate carbon-assimilation as a special function.

up with them into the more complex bodies, to be again broken down, and repeat the process,* and so on.

If, however, for any reason a lack of these carbohydrates occurs, then these amide-bodies increase for the time being, and the protoplasm suffers accordingly; in fact, it undergoes further decompositions as a result of starvation.

The evidence also goes to show that organic acids (such as malic, citric, tartaric, oxalic, &c.) are formed in the protoplasm, and accumulate in the cell-sap during these metabolic processes, as products of incomplete oxidation, and their variations in quantity depend greatly on the activity of these metabolic processes, and, therefore, on the intensity of respiration.† A fact of primary importance for us is that these organic acids increase considerably in amount under conditions which lead to less complete oxidation, and, conversely, they decrease when certain oxidation-processes in the cell are promoted. In other words, they are continually being formed and destroyed in metabolic changes, and sometimes one process, sometimes another, predominates.

As a third group of life-processes which our selected cells would exhibit, we may regard the phenomena of *growth;* processes which are intimately dependent upon *respiration* and *metabolism*, and, indeed, inseparable from them in life.

For our present purpose, it suffices to regard growth‡ as consisting in an extension of the still soft cellulose cell-walls, which tends to increase the area of the membrane at the expense of their thickness, and in a compensating increment in their thickness due to the activity of the protoplasmic lining in secreting and laying on cellulose on the inside of, or even in the structure of, the wall. Passing over the fact that the secretion of this cellulose is another manifestation of metabolic activity on the part of the protoplasm, it is important to notice that growth is only possible so long as respiration is proceeding, and so long as the cell is turgid.§ Now turgidity depends on the

* See E. Schulze, 'Landwirthschaftliche Jahrbücher,' 1876, vol. 5, p. 848; Borodin, 'Bot. Zeitg.,' 1878, col. 801; Palladin, "Ueber Eiweisszersetzung in d. Pflanzen," &c.' ('Ber. d. Deutsch. Bot. Gesellsch.,' 1888, p. 205, see p. 212). Further literature in Pfeffer, 'Pflanzenphys.,' p. 301.

† See especially Warburg, "Ueber die Bedeutung der organischen Säuren für den Lebens-process der Pflanzen" ('Unters. aus d. Bot. Inst. zu Tübingen,' 1886—88, vol. 2, pp. 53—152, where the literature is collected up to date; and Palladin, "Athmung und Wachsthum" ('Ber. d. Deutsch. Bot. Gesellsch.,' 1886, pp. 322—328), and the same on "Bildung der organischen Säuren in den wachsenden Pflanzentheilen" (*ibid.*, 1887, pp. 325—326).

‡ For a general account of growth, *cf.* Sachs, 'Lectures,' pp. 411—424 and 567—569.

§ See de Vries, 'Unters. über die mechanischen Ursachen der Zellstreckung,' Leipzig, 1877, and the literature there quoted.

presence in the cell of water under pressure: that is to say, in a turgid cell there is in the sap cavity sufficient water not only to supply all the demands of the cell-walls and protoplasm, but to keep them distended as well, and this to such a degree that the cellulose walls, with their lining of protoplasm, are positively stretched in opposition to the elastic resistance offered by the former. Recent researches have proved that this excess of water is largely due to the osmotic attraction exerted by the organic acids and their salts dissolved in the sap of the cell,* and since we have seen that the formation and destruction of these acids depend on the processes connected with oxidation and respiration, we obtain a futher glimpse into the complicated correlations here concerned. For our purpose the important points are that, during active turgescence, the growing cells tend to become very watery and their cell-walls to be thinned by stretching, and this in spite of the activity of the protoplasm in adding new materials; while bodies such as soluble amides and organic acids are being formed continuously and in relative and varying abundance, to undergo further changes in the never ending turmoil of metabolism, as already indicated.

But it is evident that these processes of respiration, destructive metabolism, and growth must sooner or later come to an end if the stores of carbohydrates fail, since these are the substances which ultimately supply the fuel for respiration, and which form the raw materials by means of which new protoplasm may be constructed; and it is well known that the plant respires and grows to death if placed in such circumstances that no new supplies of these substances are possible. We must remember that we are concerned with normal green cells, however, and we have now to consider the new set of events due to the assimilative action of the chlorophyll corpuscles to which these cells owe their colour. It is not necessary to remind you that this process of carbon *assimilation*† consists in the coming together of carbon dioxide and water in the green corpuscles, where, by means of energy obtained in certain rays of sunlight, the molecules of the carbon dioxide and water are torn asunder and eventually in part rearranged; speaking generally, we may say that some of the constituents (oxygen‡) escape, while others (carbon, hydrogen, and

* De Vries, "Ueber die Bedeutung der Pflanzensäuren für den Turgor der Zellen" ('Bot. Zeitg.,' 1879); also Palladin, "Bildung der organischen Säuren in den wachsenden Pflanzentheilen" ('Ber. d. Deutschen Bot. Gesellsch.,' 1887, p. 325). Other literature will be noticed where necessary as we proceed.

† For a general account of carbon assimilation, see Sachs, 'Lectures on the Physiology of Plants,' especially pp. 296—323.

‡ This oxygen is not active (see Pfeffer, 'Beitr. z. Kenntn. Oxydationsvorgänge,' p. 478).

oxygen) form new combinations, which result in the production of carbohydrates, which then separate from the protoplasm.*

We are here, of course less concerned with the difficulties which beset the questions, what rays of light are concerned in this process, how their energy is employed in the chlorophyll, and what part the chlorophyll itself takes directly in the process; or with questions as to the exact products formed during the putting together of the carbohydrate in the protoplasm of the chlorophyll corpuscle, and so on, than with certain well-established facts and conclusions, such as the following.

The process of building up the products obtained by the decomposition of the carbon dioxide and water in the protoplasm into carbohydrates goes on continuously in the sunlight, so long as it is sufficiently intense, and the excess beyond what is immediately required for the nourishment and respiration (*i.e.*, the maintenance of metabolic activity) of the living substances of the cell takes the final form (usually†) of starch. Free oxygen escapes all the time, and, in so far as this is not absorbed for purposes of oxidation, there and then in the cell, this oxygen goes to enrich the atmosphere. Moreover, these temporary stores of starch are continuously being transformed into soluble glucoses, by means of diastatic ferments‡ in the protoplasm; this process goes cn day and night, and its result may be easily demonstrated in the case of leaves removed from the plant after exposure to the sunlight during the day. After a few hours in a warm, dark, normal atmosphere, relatively large quantities of glucose are found in the cells, while the starch is disappearing. This glucose, I need hardly remind you, is the soluble movable form of the carbohydrates,§ and it is worked up again, so far as it is in excess of the

* The literature of this part of the subject is enormous, and dates from Priestley ('Phil. Trans.,' 1772) to the present time. It may be said to fall under four heads: (1) the nature and functions of chlorophyll; (2) the absorption of carbon dioxide and the evolution of oxygen; (3) the intensity and kind of light necessary; (4) the chemical processes which intervene between the coming together of the carbon dioxide and water and the production of the final visible product—starch. I shall, naturally, here refer only to such special literature as bears on the main subject of the present lecture.

† Sachs, 'Flora,' 1862, Nos. 11 and 21, and 1863, p. 33; also 'Bot. Zeitg.,' 1862, col. 366; Godlewski, 'Flora,' 1873, p. 378, and 'Arb. des Bot. Inst. in Würzburg,' 1873, vol. 1, p. 343. Again, Sachs, 'Arb. des Bot. Inst. Würzburg,' vol. 3, Heft 1, 1884; G. Kraus, 'Jahrb. für wiss. Bot.,' vol. 7, 1870, p. 511; Famintzin, 'Jahrb. für wiss. Bot.,' vol. 6, p. 34.

‡ Baranetzky, 'Die Stärkeumbildenden Fermente,' 1878.

§ Numerous interesting results have been obtained of late years confirming and strengthening our theory of carbohydrate assimilation: see Böhm ('Bot. Zeitg.,' 1883, col. 33), A. Meyer ('Bot. Zeitg.,' 1886, col. 81), Laurent ('Bot. Zeitg.,' 1886, col. 151), who proved that leaves deprived of starch can form it from various sugars, glycerine, &c.; also Wehmer ('Bot. Zeitg.,' 1887, col. 713), O. Löw ('Ber. d. Deutsch. Chem.

immediate requirements of the living protoplasm, into the form of reserve starch, &c., by the protoplasm.*

At certain periods, therefore, the cells may contain relatively large quantities of this soluble, nutritious, and easily oxidised glucose.

We have still to refer shortly to another set of events taking place in the normal living cells, the connexion of which with the above simultaneous functions will be obvious. This is the *passage of water* from one cell to another, a process depending essentially upon the modified evaporation—*transpiration*†—going on at those surfaces of the cell walls which are in contact with the air in the intercellular spaces, &c., and the rapidity and magnitude of whose movements depend on a variety of circumstance.

This water comes from the vascular system, by which it is brought up from the soil after being absorbed by the root-hairs, and it contains traces of the necessary mineral salts—chiefly sulphates, nitrates, and phosphates of calcium, magnesium and potassium, in small, and varying quantities—as well as dissolved gases. Whether the oxygen dissolved in the water absorbed at the root reaches the cells higher up in the plant or no, it is at least clear that the water in these cells becomes oxygenated by contact with the atmospheric air which penetrates into the intercellular spaces, *viâ* the stomata and lenticels.‡ Moreover, it is impossible to doubt that oxygen reaches the water in the cells from the assimilating chlorophyll corpuscles. However, we are not confined to inferences in this connexion, since Pfeffer has conclusively shown that free oxygen does exist in the cell-sap§ in the normal condition.

The importance of this matter for my purpose is that the move-

Gesell.,' 1886, p. 141), Bokorny ('Ber. d. Deutsch. Bot. Gesellsch.,' 1888, p. 116), who confirmed the above and proved the same for methylal, methyl alcohol, glycol, &c.; and Saposchnikoff ('Ber. d. Deutsch. Bot. Gesell.,' 1889, p. 258). The organic acids cannot be employed with the same results (see Wehmer, *op. cit.*, p. 713), though they can be absorbed and oxidised in the living cells (Warburg, *op. cit.*, pp. 112—113) more rapidly than they are decomposed outside the plant.

* See Schimper, "Unters. über die Entstehung der Stärkekörner" ('Bot. Zeitg.,' 1881, p. 881); A. Meyer ('Bot. Zeitg.,' 1880, Nos. 51 and 52).

† For the general exposition, see Sachs, 'Lectures on Physiology of Plants,' pp. 246—254, and the text-books quoted. Then Kohl, 'Die Transpiration der Pflanzen,' &c., Brunswick, 1886; Eberdt, 'Die Transpiration d. Pflanzen und ihre Abhängigkeit von äusseren Bedingungen,' Marburg, 1889. The literature is collected by Burgerstein in 'Verhandl. d. K.K. Zool.-Bot. Gesell. zu Wien,' vol. 37, 1887; vol. 39, 1889.

‡ See Godlewski's explanation of the fine air-passages which run between the medullary ray-cells and place them in communication with lenticels (Pringsheim's 'Jahrb. f. wiss. Bot.,' 1884, pp. 569—630).

§ 'Unters. a. d. Bot. Inst. in Tübingen,' vol. 1, p. 684, and "Beitr. zur Kenntniss der Oxydationsvorgänge in lebenden Zellen" ('Abhandl. der Kgl. Sächsischen Gesell. d. Wiss.,' vol. 15, 1889, p. 449).

ments of water, chiefly due to transpiration, but also incidentally caused by local decomposition, osmotic absorptions, &c., are effective in bringing about aëration of the tissues; of course this aëration (or ventilation) is not to be confounded with the movements of free gases, due to diffusion or to expansions or contractions due to changes of temperature.*

These, then, are some of the changes which are continually and continuously going on in the living cells of the normal plant. Of course I have not attempted any exhaustive list, or even a complete sketch of the structures and processes met with in living cells, the purpose being simply to bring prominently into view certain features of importance to the matter in hand.

The Death of the Cell.

The next point to consider is, what changes are observed when such cells as the above are killed.† It appears to be of little moment

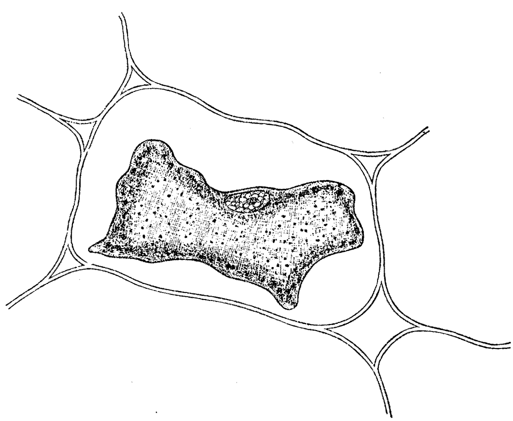

Fig. 5. A thin-walled parenchymatous cell killed by a few seconds' immersion in water at 75° C. The protoplast contracts from the cell-wall, carrying with it the nucleus and chlorophyll-corpuscles, and allowing the cell-sap to escape; the thin cellulose wall consequently becomes lax, and suffused with cell-sap. A similar result is brought about by longer immersion in water at lower temperatures (above 50° C.), or by very low temperatures, the action of poisons, &c. (Highly magnified.)

* For further discussion, see Pfeffer, 'Pflanzenphysiologie,' vol. 1, pp. 112—113, and the literature on transpiration.

† On this subject *cf.* Frank, 'Krankheiten der Pflanzen,' 1880, pp. 12—15; Detmer, in 'Bot. Zeitung,' 1886, No. 30; Pringsheim, in 'Jahrb. f. wiss. Bot.,' vol. 12, 1880 (pp. 47—50 of the separate copy); also de Vries, 'Untersuch. mechan. Ursachen d. Zellstreckung,' pp. 17—21.

how the killing is brought about, so far as the final appearances are concerned. We may place the cell, for instance, for a few minutes in hot water (say 55—80° C.), or expose it to very low temperatures, or to the vapour of chloroform, to acid gases, &c., and in each case the morphological changes are substantially the same.* In the first place, the movements of the protoplasm cease, and the granulation increases, while the whole contracts away from the cell walls into a more or less shrivelled, irregular lump. The cell-sap, previously held in the sap-vacuoles† under pressure in the turgescent living cell, now escapes, and suffuses the whole tissue, evidently because, the structure of the protoplasm being destroyed, it can no longer be kept in bounds as it was before. It would carry us too far to enter into the discussion as to what kind of changes the protoplasmic lining has undergone in its different layers; it suffices to note the fact that, whereas the living protoplasm was able to regulate the entrance of substances into the cell-sap and their escape from it, it is no longer able to do so when the cell has been killed, and the uncontrolled sap escapes as said. This sap is acid, often strongly so, and contains, among other things, certain bodies, known generally as chromogenes, which, on exposure to the air, undergo oxidation changes which result in the formation of brown colouring matters. We know very little about these chromogenes beyond the fact of their existence, but the evidence goes to show that they are unstable bodies of various kinds which are present in the cell-sap under such conditions that they are not directly oxidised by the passive oxygen dissolved in the sap; on exposure to the air, however, some substance in the sap acts as an oxygen-carrier, and they undergo the change of colour referred to.‡ The consequence of this is that the disorganised protoplasm, cell walls, &c., of the tissues thus suffused turn brown, resulting in the well-known colours of dead vegetable tissues. These changes are accelerated by the organic acids, which cause the chlorophyll grains to turn yellow, and then suffer further changes from the oxygen of the air.

It is, of course, unnecessary to remark that all the rhythmical series of processes connected with the living cell are now put an end to: respiration, metabolism, growth, assimilation have obviously ceased, as have all the other functions of the cell. Moreover, the evaporation of water is no longer controlled by the conditions imposed on it by

* This, of course, without prejudice as to the sequence of molecular changes which bring about the final result.

† See Pfeffer, 'Osmotische Unters.'; de Vries, "Studien üb. d. Wand d. Vacuolen," &c., in addition to the foregoing.

‡ See especially Pfeffer, "Beitr. zur Kenntniss d. Oxydationsvorgänge in lebenden Zellen," pp. 447—454, where the older literature is collected. The remarkable behaviour of these substances in the cell-sap suggests how extremely complex every part (even the presumably simplest) of the organism of the cell must be.

the protoplasm of membranes of living cells,* and if the weather becomes dry the dead tissues rapidly desiccate and shrivel.

In attaining the above described extreme, commonly called death, the normal living cell, in the condition commonly called health, passes through a series of vicissitudes which affect every part of it; but it is necessary to admit that the state called death and that called life, in the above discussion, are by no means definite and utterly distinct from one another—on the contrary, the very essence of life consists in its mobility, and the living cell is continually approaching and receding from the state termed death. In a certain sense, no doubt, death may be regarded as the cessation of life, but this does not help us, because the *crux* resides in determining when life ceases in the protoplasm. Of course we can lay our hands, as it were, on given cells or tissues of cells, and say these are "living," whereas others are "dead," but the difficulty is to decide when the one state passes into the other.

Between normal life, *i.e.*, the condition of affairs where the life-processes are going on actively, and the state of permanent death, then, there are all possible gradations: many of these gradations coincide with the phenomena of disease—pathological conditions—and it is towards this difficult domain that I have now to carry the discussion.

Variations in the Environment as affecting the Physiological Processes in the Host.

In describing the phenomena going on in what was termed the normal, living cell, I only hinted at the fact that variations, more or less periodic in nature, occur in the intensity of the processes, a truth which at once shows the difficulty of deciding what a normally living cell really is. But it is of the utmost importance to recognise that all the life-processes, and the changes dependent on them, are in their very nature variable. One set of factors which bring about the variations are internal and inherited, and very little is known of them beyond the fact of their existence, which is usually formally expressed by the admission that different plants differ in "constitution;" fortunately, this series of factors does not concern us at present, and it does not vitiate our general conclusions to assume that on the whole the differences in constitution between plants of the same species are so minute that they may be neglected.

The second set of factors is of much greater importance, because they give rise to pronounced and easily recognisable changes in the

* See Sachs, 'Physiologie Végétale,' pp. 253, for proof that water evaporates less rapidly from living cell-surfaces than from dead ones, and for literature (my edition is the French one of 1868).

plant. These factors are such as the following: changes of temperature, variations in the intensity of the light, differences in the amount of aqueous vapour in the atmosphere, &c., in short, the variable factors of the physical environment of the plant. That these affect the physiological processes in the cells is well known;* but what I have to do is to trace some of the effects, and show how they bring the living tissues into such conditions that they more or less readily resist or succumb to the attacks of certain parasitic fungi.

Taking the more or less arbitrarily chosen but convenient headings already employed—respiration, metabolism, growth, carbon assimilation, &c.—let us now see what kinds of effects the external agents referred to may produce.

Respiration, though it proceeds at very low temperatures,† is rendered considerably more energetic as the temperature rises, until, after a certain relatively high temperature (about 45° C.) is reached, it becomes less intense, and injury to the cells soon results, undoubtedly from damage to the structure of the living substance, owing to the excessive disturbances brought about in its metabolism. Speaking generally, we may fairly say that at temperatures near 0° to 5° C. the respiration is very slow; as the temperature rises the respiratory activity increases, at first slowly, and gradually more and more rapidly, till at 35° to 45° C. it is at its *maximum* intensity; beyond that it rapidly declines, and ceases with the death of the protoplasm at about 50° C.

Light appears to exert little or no effect on the normal process of respiration, unless relatively very intense,‡ when it may possibly promote it; but bright light may accelerate certain processes of oxidation which would otherwise have gone on more slowly.§ This much probably may be said, however: in so far as light influences oxidation processes (other than respiration) in the living cell, the action increases with the intensity of the light.|| As we shall see

* See Sachs, 'Lectures on the Physiology of Plants,' pp. 189—204, 299—308, 552—555, &c., for an introductory general account. The special literature will be noticed as we proceed.

† See Kreussler in 'Landwirthschaftliche Jahrbücher,' vol. 16, 1887, and vol. 17, 1888, for the dependence of respiration on temperature.

‡ Of course referring to ordinary daylight only.

§ See Pfeffer, 'Pflanzenphysiologie,' vol. 1, p. 376, as to possible bearing of this on decomposition of organic acids (Pfeffer, "Über d. Oxydationsvorgänge in leben. Zellen," pp. 454, 469, 472).

|| As to the effect of very intense light, see Pringsheim, "Ueber Lichtwirkung und Chlorophyllfunction in der Planze" ('Jahrb. f. wiss. Bot.,' vol. 12, 1880, pp. 84—93). It should be remarked that Pringsheim not only shows that the action is really due to light- and not heat-rays, but that the more refrangible rays (blue, &c.) are the most active (see pp. 40 and 52). These and others of Pringsheim's observations may be accepted without prejudice as to his theory of assimilation.

later on, there are some other remarkable changes going on in the cell, and connected indirectly with the action of light and respiration, but these do not probably affect the general conclusions just advanced, close as is the connexion between respiration and metabolism generally.

The question now arises as to the quantity of oxygen necessary for respiration, and as to the effects of undue accumulation of the carbon dioxide: it is too long a subject and it is unnecessary to discuss it in detail.* I need only remind you that in the absence of oxygen respiration ceases,† while it is interfered with when the amount of oxygen is much greater per unit of volume than in ordinary air, *i.e.*, when the oxygen is condensed; under ordinary circumstances, however, the free oxygen of the atmosphere amply suffices, provided it can pass readily into the cells and be renewed. Anything of the nature of stagnation must be assumed to impede respiration, whether simply from the accumulation of carbon dioxide, or other products of respiratory activity and consequent metabolism, or because sufficient oxygen-molecules do not pass into the protoplasm in a given time. Since the extremes are not nearly attained in nature, however, I pass by this subject with the remark that in proportion as the intercellular passages or other communications with the atmosphere‡ become blocked by condensed water, for instance, the ventilation of the plant—and therefore its respiration—may suffer§ for the time being simply on account of the slower diffusion of the gases, carbon dioxide and oxygen, from one part of the plant to another.

Coming now to the subject of destructive metabolism, we find that it is affected by external factors; in the first place, by whatever affects respiration, and therefore the foregoing remarks apply to metabolism generally. This is especially so in the case of temperature, and the statements already given may serve broadly with respect to metabolism as a whole. A few details are of importance, however. We have

* For further details, *cf.* the text-books already cited, *e.g.*, Pfeffer, vol. 1, p. 377.

† We are of course not concerned with so-called "intra-molecular" respiration (*cf.* Pfeffer, vol. 1, pp. 370—374).

‡ See Russow, "Zur Kenntniss der Hölzer," &c., in 'Bot. Centralbl.,' 1883 vol. 13, p. 136.

§ It is no uncommon event, even in England, to see the intercellular passages of leaves blocked with suffused water after a cold night, but the phenomenon is much commoner in the tropics, and occurs quite generally in the hill country in Ceylon, for example. As the temperature rises during the morning, the water quickly evaporates and the leaf loses its dark, suffused, limp appearance, and becomes normal. Of course, the phenomenon is due to proportionally more water being absorbed from the relatively warm soil than the cool air can take up. See also Pfeffer, 'Pflanzenphys.,' vol. 1, p. 172, and the literature concerning the ascent of water in plants (collected in Marshall Ward, 'Timber and some of its Diseases,' 1889, pp. 59—141).

spoken of two sets of bodies among the many which are produced during the metabolic processes of the cell—the organic acids and the amide-substances. It appears from the evidence to hand that organic acids are not only formed, but are also subsequently oxidised, in the cell, and it is only to be expected that this process of decomposition of the acids is also promoted by raising the temperature, and conversely,* and such is the case; these acids increase during the night and diminish during the day, and one important factor in the processes is temperature. The *optimum* of increment of organic acids in the plant occurs at somewhat low temperatures†—*e.g.*, about 10° C. to 15° C.; while the *minimum* coincides approximately with that of respiration (near 0° C.), and the acids cease to increase—or, rather, they are decomposed as fast as, or faster than, they are produced—as the temperature rises to 35—40°.

With respect to the effects of light on metabolism, reference may be made as to what has already been said as regards its promoting certain processes of oxidation in the cells,‡ and to what follows on assimilation. The part played by oxygen also has been adverted to; metabolism in the ordinary course of events depends on respiration, and all that affects the latter affects it. In the absence of free oxygen, conditions of intense destructive metabolism are eventually set up, the details of which we need not discuss.§ If plenty of non-nitrogenous food materials are present, the metabolism goes on for some hours as usual, but soon the starving protoplasm undergoes more and more profound changes, resulting eventually in a loss of proteid substances.

It is important to bear in mind that in the cells containing chlorophyll the free acids diminish in daylight, and increase as the light fades and in darkness, no doubt because there is less oxygen in the absence of that set free by the chlorophyll corpuscles; these acids also decrease in proportion as the temperature rises, and increase as it falls. It is also important to be clear in this connexion as to the fact that two processes are going on simultaneously—on the one hand, organic acids are being formed as products of incomplete oxidation in the respiratory processes, and, on the other, they are being further oxidised and decomposed when the temperature is high and the light bright.‖ Whether at any given moment the amount of acid present

* See Warburg, 'Unters. aus d. Bot. Inst. zu Tübingen,' vol. 2, Heft 1, 1886, p. 102.

† Warburg, *op. cit.*, pp. 71 and 102, confirming the results obtained by de Vries (literature quoted).

‡ See Pfeffer, 'Ueb. die Oxydationsvorgänge,' &c., pp. 419 and 454.

§ See, however, Palladin, "Ueber Eiweisszersetzung in den Pflanzen bei Abwesenheit von freiem Sauerstoff" ('Ber. d. Deut. Bot. Gesellsch.,' 1888, p. 205).

‖ That the connexion with light depends on the access of oxygen set free in

is larger or smaller depends on the resultant action of these processes. Anything which interferes with oxidation promotes the accumulation of organic acids, whereas those changes which lead to increased oxidation in the cells are followed by a decrease of acids.

Now a few words as to growth, and its dependence on external factors. Apart from the thickening of the cell-walls, which comes afterwards and depends on the addition of materials formed by the protoplasm,* the principal phenomenon that concerns us is the extension of the cellulose membranes. This process is promoted by moderately high temperatures, and retarded by low ones and by very high ones,† in accordance with respiration and the general metabolism of the cell; the curves are not quite the same, because respiration begins at temperatures too low for growth, and goes on rising in intensity to temperatures at which growth begins to decline; still the connexion is very close, and the dependence of growth on respiration and metabolism implies this.

Light is usually considered to have a retarding effect on the growth of the cells. Apart from the possibility that there may be a more direct action of light on the extensibility of cell-walls or of cells generally, by its effects on the protoplasm at the spot, one way in which this retarding effect may be brought about is in connexion with the turgidity of the cells. Without concerning ourselves with the general discussion of the whole subject, which would be a very long one, it seems, at least, clear that in the ordinary course of events light exercises some retarding action on growth by extension; what, if any, connexion exists between this phenomenon and the observed diminution of the organic acids in the cells (and we have seen that their turgidity depends on these acids and their salts) in daylight still needs investigation, and the same may be said as regards the influence of temperature in relation to growth and the production of acids. It is customary to regard the retarding action of light on the extensibility of the cell-wall as a complex phenomenon of irritability,‡ and it is by no means certain that such is not the case; meanwhile we simply accept the facts that in ordinary bright light the extension of the growing parts is retarded, that this is connected with diminished turgidity, which in its turn is dependent on the pressure in the sap of substances capable of retaining the

carbon assimilation, and not on any direct action of the rays of light, can hardly be doubted (see Warburg, *op. cit.*, pp. 77—92).

* For details see Strasburger, 'Uber den Bau und Wachsthum der Zellhäute' and "Ueber das Wachsthum vegetabilischer Zellhäute" ('Histologische Beiträge,' No. 2, 1889).

† Sachs, 'Physiology,' pp. 194 and 553.

‡ See Vines, 'Physiology of Plants,' p. 398; but *cf.* also Wortmann, 'Bot. Zeitg.,' 1887, Nos. 48—51, especially col. 808—810.

necessary water. If we accept, with de Vries,* that these substances are chiefly the organic acids and their salts, then we may expect the study of influence of light in promoting the decomposition of organic acids in the plant to give more information on these matters. The same remarks apply with regard to the influence of variations in temperature.

Growth is, of course, impossible without water, and the transpiration current supplies this to the osmotically active cells. In nature, the quantity of water at the disposal of these cells varies enormously, not only with the quantities at the disposal of the root-hairs, but also with the rapidity of the transpiration influenced by the atmosphere. On the whole, given favourable temperature, and other circumstances, growth in length is most active in damp weather, when the quantities of water in the cells are relatively very large ; it is retarded in hot, dry weather, because the loss of water is sufficiently extensive to diminish turgidity.

Passing now to *carbon assimilation*, I come to the subject which offers most interest for our enquiry. Assimilation is also to some extent influenced by temperature, although in a very different manner from respiration ;† and the influence of even large variations in temperature may be masked by the effects of small variations in other factors, especially light. Assimilation takes place at low temperatures whenever respiration is possible, but the temperature curve for assimilation in ordinary bright sunlight is steeper than that for respiration, and at higher temperatures (say, 30° C. and above) where respiration is not yet most active, assimilation is already beginning to decline. In the blackberry, for instance, whereas assimilation is most active at between 29° and 33° C., respiration goes on becoming more and more energetic to 46° C., at and beyond which its effects are of course dangerous to the plant.‡ On the whole, we may conclude that at low temperatures, say, 5° to 10° C , on a bright spring morning, assimilation is relatively more active than respiration, whereas at higher ones—30° to 40°—the reverse is distinctly the case.

The effects of variations in the intensity and kind of light on assimilation have been much studied, and may be summed up generally for our purposes as follows.

With ordinary solar light, as it reaches the plant on a clear day in the open, the activity of assimilation increases nearly in proportion to the intensity§ of the light ; this is usually expressed by saying, the

* 'Unters. über d. mechan. Ursachen d. Zellstreckung,' 1877, and 'Bot. Zeitg.,' 1879, col. 848.

† See Kreussler, 'Landwirthschaftl. Jahrb.,' vol. 16, 1887, and vol. 17, 1888.

‡ See Kreussler, *loc. cit.*, 1887, p. 746.

§ The word must not be pushed too far as to meaning, in the absence of any satis-

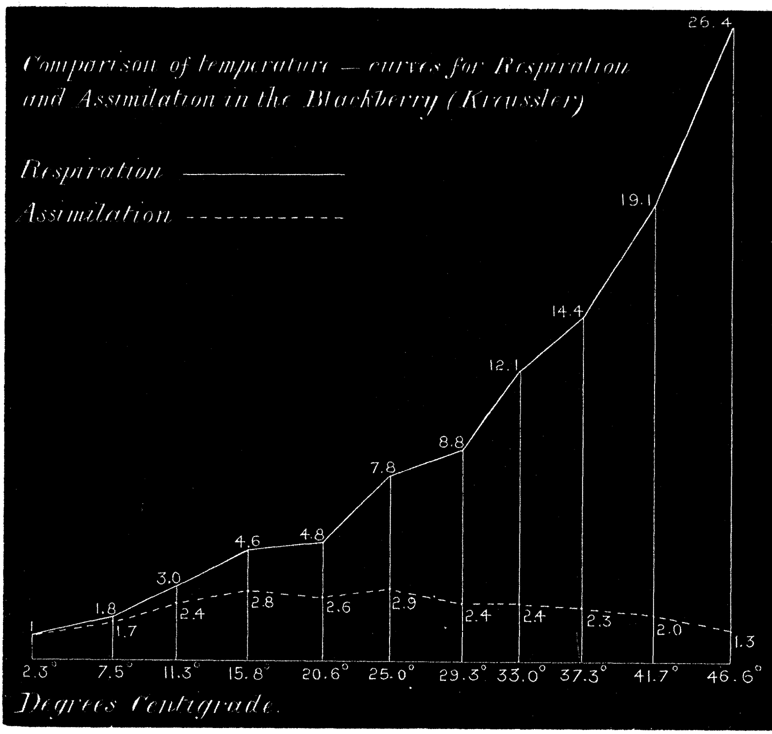

FIG. 6. Diagram constructed to show the comparative effects of equal increments of temperature on respiration and assimilation respectively, according to Kreussler's data. The base line has marked off on it a number of intervals corresponding to so many degrees centigrade, as denoted by the figures; on the ordinates from these points are measured distances corresponding to Kreussler's figures—numbers representing the comparative intensity of the functions in question, if that at the lowest observed temperature is taken as unity.

more light the plant can get, the better. There is evidence to show that, as might be expected, light of great intensity concentrated by means of a lens, &c., on to the assimilating apparatus, produces destructive pathological changes; but we may also infer from everyday experience with shade-plants (*e.g.*, camellias) that the light may be too intense for normal assimilation to go on,* and such is the case.

Another point of importance is the kind of light which reaches the

factory mode of estimating "brightness," "intensity," "quantity," &c., of light (see Sachs, 'Phys.,' pp. 301—302).

* See Famintzin, 'Bull. de l'Académie de St. Pétersbourg,' vol. 26, 1880, col. 296—314. Also Reinke, 'Bot. Zeitg.,' 1883, No. 42, with literature.

plant. I need not remind you that some rays of the solar light, especially some of the less refrangible (orange and red) rays, are more concerned in the process of assimilation than others, and, although we cannot here stop to discuss this matter in detail, I may point out that, as different rays of light are absorbed or reflected in the atmosphere, we may have variations in this connexion of more or less importance to the plant. The experience of photographers shows that the different thicknesses of the atmosphere through which the light has to pass, reflection from a cloud as contrasted with the "blue sky," &c., all exert influence on the composition of the light, and in prolonged cloudy, dull weather or fogs this factor may add its effects to those due to the mere dilution of the light as a whole.

But the fundamental nature of the necessity for a suitable intensity of light of the right composition is best brought out in studying the effects of low intensities of light on the green organs of plants.

As is well known, the general effect of keeping a plant in the dark is to induce a condition known as etiolation.* The whole plant becomes pale yellow or colourless, and has a curiously translucent, watery appearance; the internodes are excessively long, while the leaves, on the contrary, are usually small and crumpled. Closer investigation shows that each cell of the internodes is abnormally elongated, its cell-wall thinner than usual, and its chlorophyll corpuscles small and wanting the green chlorophyll. If we examine the vascular bundles, they are found to be deficient in firmness, because the substances which normally go to thicken their walls have not been forthcoming.

Everything about the etiolated shoot indicates tenderness, and as a matter of fact such shoots are very ill-adapted to withstand the ordinary exigencies of plant life. Undoubtedly the chief cause for this weak condition is the absence of the light necessary for the purposes of assimilation; the carbon dioxide may be present, and even the fully green chlorophyll could be developed by a few hours' exposure to feeble light, but these do not suffice for the construction of the materials such as glucose, starch, &c., necessary to enable the protoplasm to keep the tissues normal.

Nevertheless, the other functions of the cell are being carried on with remorseless pertinacity. The oxygen of the air enters the protoplasm, establishes its usual combinations, and carbon dioxide and water are given off to the air. The chemical changes known collectively as metabolism proceed, and result in the addition of substances to the cell-sap which were not previously there. To an extent more marked than ever before, the turgid cells may be elongating, and this

* See Sachs ('Bot. Zeitg.,' 1863, supplement, and 1865, col. 117, &c.); G. Kraus ('Jahrb. f. wiss. Bot.,' vol. 7, p. 209; Godlewski ('Bot. Zeitg.,' 1879, col. 81); de Vries ('Bot. Zeitg.,' 1879, col. 852); Godlewsk (Biol. Centralbl.,' 1889).

brings us to note that the key to the condition of affairs is the fact that the dry weight of the etiolated shoot is decreasing: every molecule of carbon dioxide which comes away lessens the dry organic substance of the plant, and no restoration of such substance is possible in the absence of light.

In other words, then, the etiolated plant is growing to death, at the expense of what organic carbon-compounds it possessed at the beginning.

Assimilation is, of course, profoundly affected, like every metabolic process, according to the relative amounts of oxygen and carbon dioxide in the air, and although it never happens in nature that the extremes are approached, nevertheless experiments on this subject have led to interesting results.*

The quantity of water present in the plant and its atmosphere and the rapidity of the transpiration current undoubtedly affect the process of assimilation in a high degree. Not only is water needed for the molecular processes concerned in the act of assimilation, and not only does the supply of materials to the protoplasm depend mainly on the transpiration current, but, as we have seen, the aëration of the intercellular passages, and consequently the movements of gases generally are affected.

It has long been known that the quantities of carbon dioxide absorbed, and of oxygen evolved, in the process of assimilation, vary with the age of the leaf or other organ concerned, and Kreussler has shown that one reason for these variations is the quantity of water present in the tissues at the time. In fact, an essential cause of variations in assimilation exists in the differences in the water contents of the tissues,† and it is no doubt largely due to the want of water that older leaves assimilate so unequally—they are unable to rapidly restore the equilibrium between losses and gains when it is seriously disturbed.

As for transpiration itself, and all the movements of water correlated with it, it is well known that the various factors of the environment affect it profoundly.

Apart from the more obvious relations‡ between transpiration and the temperature of the atmosphere, and the quantity of aqueous

* See Godlewski, "Abhängigkeit der Stärkebildung in den Chlorophyllkörnern von dem Kohlensäuregehalt der Luft" ('Flora,' 1873, p. 378); also in 'Arb. des Bot. Inst. in Würzburg,' 1873, vol. 1, p. 343. Further, Pringsheim, "Ueber die Abhängigkeit der Assimilation grüner Zellen von ihrer Sauerstoffathmung," &c. ('Sitzungsber. d. Kgl. Preuss. Akad. der Wiss. zu Berlin,' 1887, No. 38, pp. 763—777).

† Kreussler, "Beobachtungen über die Kohlensäure-Aufnahme und -Ausgabe der Pflanzen," II ('Landwirthsch. Jahrb.,' vol. 16, 1887, especially pp. 728—30).

‡ See the text-books referred to, especially Pfeffer, 'Pflanzenphysiologie,' vol. 1, pp. 146—150.

vapour in it, it must be borne in mind that many events concur in promoting or retarding it. The stomata, for instance, open widely in bright sunshine and close in the dark,* a matter of great importance in controlling transpiration, as must be concluded from the researches of Garreau and von Höhnel.† Other effects are traceable to the influence of the wind shaking the plant, and to the quantities of mineral salts, &c., in the soil, but it would carry me too far to discuss further instances.

The principal effects of obstructed transpiration may be shortly compared with those due to want of light—the watery tissues are strikingly like those of an etiolated plant, and we may look upon a shoot growing in a saturated atmosphere as presenting all the chief features of one growing in darkness.‡ Its cells are extremely turgid, with watery, soft, thin walls, and acid cell-sap; its vascular bundles feebly developed and hardly lignified; and, as before, it is ill adapted to withstand the exigencies of the ordinary environment.

All such plants or organs are, so to speak, in a permanently young condition.

The Effect of the Preceding Variations in "Predisposing" the Host to Disease.

If we put together the results of the preceding discussion, it is evident that a plant may vary within very wide limits of the condition we term health. No doubt this needs no proof to the minds of most of my hearers, but the point I wish to emphasise is that, in some of its deviations from the normal, the plant offers conditions to an attacking parasite which may be at one time favourable, at another not.

Suppose the case of a herbaceous plant growing under the following circumstances in July: the temperature has been high, and the daily supply of solar light abundant during the previous four or five weeks, and everything has been going on admirably, so far. Suddenly the weather changes—the temperature falls, rain sets in, and for many days heavy clouds obscure the sun. If this markedly different, dull, cold weather continues, we may have the following condition of affairs more or less realised, as is well known to those who observe cultivated plants closely.

Transpiration being lowered in activity, the whole plant tends more and more to be suffused with water; the stomata are nearly closed,

* See Sachs, 'Lectures on the Physiology of Plants,' pp. 248—250, and Strasburger, 'Das Botanische Practicum,' 2nd ed., 1887, pp. 88—90.

† See Pfeffer, 'Pflanzen-Physiologie,' vol. 1, p. 144.

‡ Vesque and Viet, "Influence du Milieu sur les Végétaux" ('Ann. d. Sci. Nat.,' 6 Sér. (*Botanique*), vol. 12, 1881, p. 167).

the cell-walls bounding the inter-cellular passages and the air in the passages themselves are thoroughly saturated with water and aqueous vapour respectively, and the movements of gases must be retarded accordingly, turgescence is promoted, and the water contents accumulate to a *maximum*, owing to the disturbance of equilibrium between the amounts absorbed by the active roots in the relatively warm soil and those passing off into the cold damp air; much more water is absorbed by the roots in the relatively warm soil than passes off as vapour in equal periods of time. An enhanced wateriness of the whole plant, then, is one result.

But the low temperature, feeble light, and partially blocked ventilation system have for a consequence a depression of respiratory activity and the absorption of oxygen generally. Enough oxygen gas finds its way slowly into the cells to keep the life-processes going, of course, but not enough to complete the oxidations and decompose the organic acids, at the prevailing low temperature, so rapidly as before,* and thus another consequence is a tendency to the accumulation of organic acids. According to de Vries, however, the increase of organic acids must make itself effective in enhancing the turgidity of the cells, and no doubt it does so to a certain extent; beyond a certain point, however, it is more likely to increase the permeability of the protoplasm,† and we may even suppose small quantities of the acids to filter out even to the watery cell-walls.‡

Partly due to the low temperature and the depressed gas-interchange, but far more owing to the feeble light, the process of assimilation will be less active than previously. This will not be immediately felt if, as will probably be the case, there are large quantities of temporary reserves in the leaves and internodes; but it may react indirectly on the processes of oxidation and respiration, inasmuch as less free oxygen is evolved in the cells than would be the case in bright weather. As the temporary stores of starch disappear, however, the cells become more and more surcharged with glucose, together with organic acids, and it depends on several circumstances, especially on how rapidly growth is going on (*e.g.*, in the parts below ground), whether this glucose in solution passes away, or is used up slowly or rapidly; if it cannot move, or only extremely slowly, then we have the case of tissues surcharged with water containing organic acids and glucose in solution. It may be surmised

* See Warburg, *op. cit.*, especially pp. 73—77, and 126.

† See Pfeffer, "Ueber Aufnahme von Anilinfarben in lebenden Zellen," in 'Unters. a. d. Bot. Inst. zu Tübingen,' vol. 2, 1886, pp. 296 and 329, for proof that dilute acids can traverse without permanently injuring the protoplasm.

‡ Pfeffer showed, for instance, that methyl-orange, after being taken up in the living cell and held there by the protoplasm, can be made to diffuse out again if a little citric acid is imbibed ("Üb. Aufnahme," &c., *op. cit.*, p. 293).

that the increased amount of organic acids is favourable rather than otherwise to the ferment processes which lead to the conversion of the starch into glucoses.* How far the protoplasm will allow the watery solution of glucose to escape, owing to its increased permeability, cannot be determined, but it is at least probable that some may reach the cell-walls. In any case, we have the cells flooded with a dilute solution of organic acids and glucose, and the controlling protoplasm becoming less and less capable of retaining the excess.

The turgid condition of the cells, and the diminished intensity of the light,† will favour growth, and, in spite of a comparatively low temperature, the organs may be extending more or less rapidly or slowly. If so, the tendency will be for the very watery cell-walls to become relatively thinner than usual, as well as watery, because the ill-nourished protoplasm does not add to the substance of the wall in proportion. This being so, we have the case of thinner, more watery cell-walls acting as the only mechanical protection between a possible fungus and the cell contents.

But this is by no means all that has to be considered, when the conditions remain as above described. Sooner or later the glucose begins to fail, either because it has been directly employed for the support of the metabolic processes in the protoplasm in the immediate neighbourhood, or (less probably) because it has been re-converted into starch,‡ or other reserve carbohydrates by the leucoplasts in the cells of the roots, tubers, &c., at a distance. Now, as soon as a want of carbohydrates makes itself evident in the destructive metabolic processes accompanying growth, the accumulation of substances like asparagin, leucin, &c., is apt to occur,§ as products of the decomposition of the proteids. Under more normal conditions, as we have seen, these amide-bodies would be worked up again with carbohydrates into new constituents of living protoplasm, but they now begin to accumulate.

The net result of the foregoing changes amounts, shortly put, to the following:—Under certain circumstances the parenchymatous tissues of the living plant may be in a peculiarly tender, watery condition, where the cell-walls are thinner and softer, the protoplasm

* Baranetzky, 'Die Stärkeumbildenden Fermente,' 1878; Brown and Heron, 'Journ. Chem. Society,' 1879; Detmer, 'Das Pflanzenphysiologische Praktikum,' 1888, p. 198.

† So far as the *composition* of the light is altered, it will probably favour growth, because the more refrangible rays are fewer when the light has to traverse a thick atmosphere.

‡ See Schimper, 'Bot. Zeitg.,' 1880, col. 881; and A. Meyer, 'Bot. Zeitg.,' 1880, Nos. 51 and 52.

§ See Palladin, "Ueber Eiweisszersetzung in den Pflanzen" ('Ber. d. Deutsch. Bot. Gesellsch.,' 1888, p. 205); and for older literature, Pfeffer, 'Pflanzenphysiologie,' vol. 1, pp. 298—301, and further literature quoted.

is more permeable and less resistant, and the cell-sap contains a larger proportion of organic acids, glucose, and soluble nitrogenous materials than usual. When the external conditions become more favourable—the temperature higher, the air drier, and the sunlight more powerful—increased transpiration and respiration lead to more normal metabolic activity, for which energetic assimilation provides the materials. Of course, all kinds of combinations are possible in detail, but when dull, cold, wet weather prevails for some time, after a period of bright, hot, and dry weather in the early summer, we are very apt to have herbaceous plants in such a condition as that sketched.

This being so, I have now to show how the chances of a suitable fungus are increased, if it happens to start its parasitic life on such a host in such a condition.

Botrytis *and other Fungi as Agents of Disease, and their Dependence on the Condition of the Host Plant.*

Let me first proceed to call your attention to a parasitic disease of a very extraordinary kind, though caused by a fungus belonging to a well-known and widely-spread family. This disease, and the fungus in question, may be met with in nearly every garden and greenhouse all the year round, and is quite common in the open fields and lanes of this country and elsewhere in Europe. In the form generally met with, the fungus has been placed in a separate genus known as *Botrytis*, though, in the few cases that have been thoroughly worked out, it has been proved that the mould-like *Botrytis* is only the conidial form of certain higher ascomycetous fungi belonging to the *Pezizas*, and which agree in developing sclerotia. As we are not concerned with the details of the whole life-history of this group, I shall purposely avoid further reference to the higher stages of development, confining our attention chiefly to the *Botrytis* stage.*

On dead and dying leaves, twigs, fruits, &c., of plants from all parts of the world, in the open and in greenhouses, in Europe and elsewhere, there is often to be observed an ashen-grey mould, superficially not unlike the *Phytophthora* of the potato-disease. It appears under various slightly different aspects as regards the shade of colour, the length and degree of branching of the conidiophores, and the size and shape of the conidia, and many different species have been figured and described, some good, many bad, according to the variations in colour, size, &c., referred to, and the substratum on which the mould is found growing.

It sometimes happens, however, that this same mould is found

* For further details as to the morphology, &c., *cf.* de Bary, 'Comp. Morph. and Biology of the Fungi,' &c., especially under the heading *Peziza Fuckeliana.*

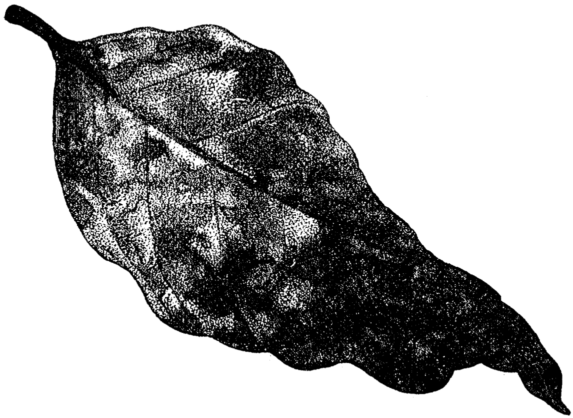

Fig. 7. A dead leaf infested with moulds, especially with *Botrytis*, as shown on the grey patches. (Natural size.)

spreading more or less rapidly from dead and dying parts of a plant to the assumed healthy organs, and it has been customary to look upon this as a secondary phenomenon due to the "dying-off" of the adjoining parts, the fungus spreading to them as they died. No one questioned the saprophytic nature of the *Botrytis*,* and so the matter stood for a long time. Gradually, however, it came to light that various forms of this *Botrytis* appear as phases in the life-history of certain sclerotium-bearing *Pezizas* which were associated in a manner suspicious, to say the least, with epidemic diseases of rape,† clover,‡ hemp,§ onions,|| hyacinths¶ (also *Scilla*, *Narcissus*, *Anemone*, &c.), balsams,** *Carex*, rice, and many other plants.

Further, this mould was found causally associated with the rotting

* Of course I am referring to the modern definition of the genus *Botrytis*, after its separation from the totally different Peronosporeæ (see 'Annals of Botany,' vol. 2, p. 357).

† See Coemans in 'Bull. Acad. Roy. de Belgique,' Sér. 2, vol. 9, 1860, p. 62; and Frank, 'Krankheiten der Pflanzen,' 1880, pp. 531—537.

‡ Kühn, 'Hedwigia,' 1870, No. 4, p. 50; Sorauer, 'Pflanzenkrankheiten,' vol. 2, 1886, pp. 283—288; Rehm, 'Die Entwickelungsgeschichte eines die Kleearten zerstörenden Pilzes,' Göttingen, 1872.

§ Tichomiroff, in 'Bull. Soc. Nat. de Moscou,' 1868, 2 (see Hoffmann's 'Mykol. Berichte,' 1870, p. 42).

|| See Frank, *op. cit.*, p. 540, and Sorauer, 'Oesterr. Landwirthsch. Wochenbl.,' 1876, p. 147, and 'Pflanzenkrankheiten,' vol. 2, p. 294.

¶ Meyen, 'Pflanzenpathologie,' 1841, pp. 164—172; and Wakker, in 'Bot. Centralbl.,' 1883, vol. 14, p. 316.

** Frank, *loc. cit.*, p. 544.

of many fruits, such as pears and apples,* grapes,† cranberries,‡ &c., and on chestnuts.§ In short, even the forms of *Botrytis* which were most persistently regarded as saprophytic have now been shown to enter living plants and cause parasitic diseases in them,|| and complaints of such epidemics are occasionally heard from various parts, as a rule, however, the disease is sporadic, and I now proceed to describe its symptoms.

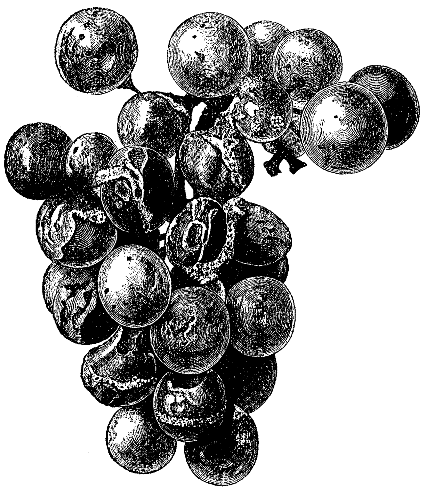

FIG. 8. A bunch of "mouldy" grapes infested with *Botrytis cinerea*. The ravages of the fungus cause the skin to rupture, and the fruits to shrivel from loss of water; other changes in the substance of the contents are referred to in the text. Patches of the conidiophores are seen on the exterior (Müller-Thurgau).

Small reddish-brown spots appear on the leaves, pedicels, ripening fruit, or other organ attacked; these enlarge and spread, and the parts turn brown, shrivel up, and rot off or dry up, according to the state of the weather. In some cases the whole plant gradually turns

* Sorauer, 'Pflanzenkrankheiten,' vol. 2, p. 298.

† See especially Müller-Thurgau, in Thiel's 'Landwirthsch. Jahrb.,' vol. 17, 1888, pp. 83—160, on "Edelfäule."

‡ See especially Woronin, 'Mém. de l'Acad. de St. Pétersb.,' vol. 36, No. 6, 1888.

§ Kissling, 'Zur Biologie der *Botrytis cinerea*,' Bern, 1889, p. 14 (where also the literature is collected).

|| *E.g.*, *B. cinerea*, the conidiophores of *Peziza Fuckeliana* (see de Bary, 'Comp. Morph. and Biol. of Fungi,' p. 380), is now known to be capable of producing epidemic diseases in vines, gentians, &c.

yellow and dies, more often only a part of it goes,* and in many cases the disease is confined to individual organs—leaves, flower-buds, fruit, &c., as the case may be. When the disease occurs amongst stored chestnuts, carrots, parsnips, &c., the tissues become speckled, and in many cases this spreads till they are rotten throughout; and similarly with stored bulbs, corms, and tubers, &c.

Wherever the disease is rampant we find the colourless, septate, branched fungus mycelium in the dead and dying tissues, and usually emitting hyphæ, which grow into the damp air and bear the conidia in abundance. In some cases, however, these aërial conidiophores have not been observed,† and the habit of producing them appears to be lost, though in every other respect the behaviour of the mycelium is the same in all the cases thoroughly examined.

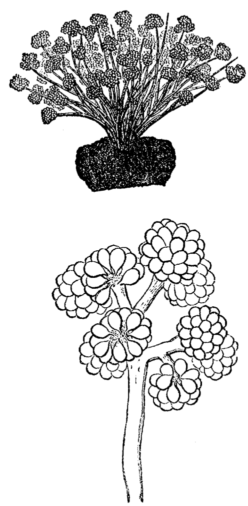

FIG. 9. *Botrytis cinerea.* The upper figure represents a tuft of the conidiophores breaking through the epidermis of a grape (magnified); the lower one is one of the conidiophores still more highly magnified.

Some very remarkable facts have come to light during the last few years concerning this mycelium and the conidia; and as all the species or forms which have been thoroughly examined agree essentially in their physiological behaviour, I need no longer trouble you

* A curious fact is sometimes observed—the small brown spot suddenly ceases to spread, and the hyphæ may be found in it in a dried-up, dormant condition for weeks. See also 'Annals of Botany,' vol. 2, 1888, p. 356, and figs. 51—54.

† *E.g.*, in de Bary's *Peziza Sclerotiorum* (Lib.). See "*Sclerotinien und Sclerotinien-Krankheiten*" ('Bot. Zeitg.,' 1886, col. 424).

with references to any special forms, excepting in so far as the citation of authorities necessitates this.

In the first place, the mycelium and conidia are not only capable of growing and flourishing in artificial nutritive media, but they often refuse to do otherwise—at least while young. If the conidia are sown in such media as the juice of grapes or other fruits, or in solutions containing an organic acid, sugar, asparagin, and traces of mineral salts, enormous cultures may be made for weeks, and millions of new conidia, sclerotia, &c., obtained, provided certain conditions are fulfilled. Among these conditions are the following:—The temperature must not be high, and may be relatively low (best about 15° C.); the solution must not be alkaline or neutral, but should be somewhat acid;* sugar of some kind—and preferably a glucose—must be present; and the nitrogenous materials may be offered as asparagin or peptone with advantage.

It will be noted that just those external climatic conditions which we have seen to be disturbing to the well-being of the green host-plant are either favourable to the fungi we are concerned with, or are at any rate not in the least inimical to their development.

Thus the oxygen respiration of the fungus goes on at all temperatures from 0° C. to 30° C. and higher, and, although we still want information as to details, experiments have shown that the mycelia flourish at temperatures considerably below the *optimum* for higher plants.†

Moreover light, so indispensable for the carbon assimilation of the green host, is absolutely unnecessary for the development of the fungus.‡

Then, again, the dull, damp weather and saturated atmosphere, so injurious to higher vegetation if prolonged, because they entail interference with the normal performance of various correlated functions, as we have seen, and render the plant tender in all respects, are distinctly favourable to the development of these fungi.

Consequently the very set of external circumstances which make the host-plant least able to withstand the entry and devastation of a parasitic fungus like *Botrytis*, at the same time favour the development of the fungus itself.

As already said, it had long been assumed that these forms of *Botrytis* are saprophytes, and the ease with which they may be culti-

* See Marshall Ward, "A Lily Disease" ('Annals of Botany,' vol. 2, 1888, p. 334); also *cf.* de Bary ('Bot. Zeitg.,' 1886, col. 400).

† See also Hoffmann ('Jahrb. f. wiss. Bot.,' vol. 2, 1860, p. 267) and Zopf. "Encyklopædie der Naturwiss." (Schenk's 'Handbuch,' vol. 4, 1889, pp. 471—472).

‡ According to Klein ('Bot. Zeitung,' 1885, col. 6), the conidia of *Botrytis cinerea* are only developed in the darkness of night, but this is certainly not the case with other species.

vated in artificial solutions, as above, tended to support that view: moreover, many attempts to directly infect living plants with the conidia failed—the conidia, if merely placed in a drop of water on a healthy leaf, simply germinated and died, and very often nothing more came of it. Nevertheless, odd instances of infection were recorded here and there, and the whole matter became a great puzzle,* until several points of startling importance came to light.

In the first place it turned out that, although the germinal tubes of certain of the *Peziza*-forms could not penetrate into the living leaf of the host directly—whereas they plunged forthwith into the tissues of a dead organ†—nevertheless the *mycelium* developed from such spores, provided it was vigorous and well nourished by previous culture as a saprophyte, could do so, but in many cases only provided the tissues of the host were in a favourable condition. This last proviso was found to be necessary, because in some cases the mycelium easily infected young growing internodes, &c., but could not penetrate into the more fully developed older parts of the same plant.‡ This threw some light on the curiously capricious behaviour of the fungus in green-houses, where seedlings, cuttings, young internodes, &c., were often attacked and destroyed, while older parts escaped, though without any regularity of behaviour.

The key to the mystery appeared to be offered when it was discovered that the invigorated mycelium, well nourished by cultivation in a solution such as that mentioned above, excretes a ferment which possesses the power of swelling and dissolving cellulose, and that this ferment is formed at the tips of the hyphæ,§ and thus enables them to enter the cell-walls, as they were actually seen to do. It becomes intelligible now why these hyphæ sometimes can and sometimes cannot quickly enter the cell-walls of a plant: when the cell-walls are thin and watery, and especially if small quantities of organic acids are present, the fungus hyphæ can easily attack and dissolve them, but in cases where they are thick and tough, owing to paucity in water and no traces of acids, the hypha has no chance. Just such differences as these would occur in the case of young and old organs respectively, or of partially etiolated or thoroughly matured tissues respectively.

But in addition to piercing the walls, and at first living in the

* We shall see that the occasional infection depends on (1) condition of host, (2) whether any soluble food-materials pass from the leaf into the drops of water, and (3) the state of the conidia.

† See de Bary, "Ueber einige Sclerotinien und Sclerotinien-Krankheiten" ('Bot. Zeitung,' 1886, col. 410).

‡ See de Bary, 'Bot. Zeitg.,' 1886, col. 440—441.

§ See Marshall Ward, "A Lily Disease" ('Annals of Botany,' vol. 2, pp. 339—343).

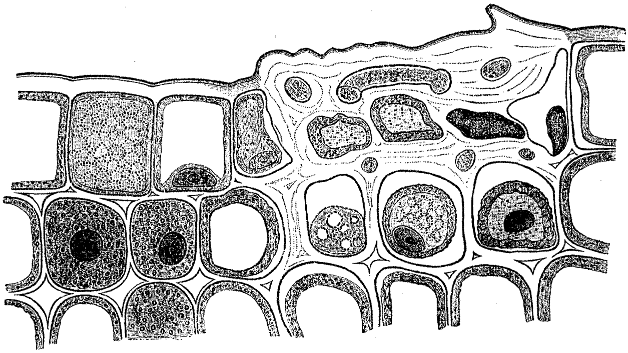

FIG. 10. Portion of a transverse section through an infection-spot in the tissues of snowdrop (such as that at *a* in fig. 11), showing the swollen cell-walls with hyphæ of *Botrytis* in them. The cell-contents also show changes; the protoplasm contracts, dies, and turns brown, and stains less and less readily the further the changes proceed; the cell-sap escapes and suffuses the cell-walls; the nucleus is the last to succumb. The above changes are exhibited by cells some distance away from the hyphæ, and are the less pronounced the further away the cells are. The colour reactions are of course not reproduced. (Very highly magnified.)

cellulose substance,* the hyphæ also excrete a soluble substance which kills the protoplasm (with which they are not in contact) of the cells in the immediate neighbourhood: whether this substance is a separate zymase, or whether it is the same soluble ferment as that which swells the cellulose, is not clear, or whether the protoplasm simply dies after excessive plasmolysis due to water passing into the swollen walls, but it is clear that some such poisonous action is exerted at a little distance from the tip of the hypha, and therefore by means of a soluble poison or zymase of some kind. It is difficult to decide what this poison is, and the following questions arise:—first, Is the poison the same zymase as that which causes the swelling and solution of the cellulose? This must be denied provisionally, at any rate, because if sections of the tissues are put into solutions containing extracts of the mycelium which have been previously boiled for a minute or two, the protoplasm contracts and dies much as before, though the cellulose walls no longer swell as before because the zymase has been killed by the boiling. This experiment is not quite conclusive, because the contraction of the protoplasm may be due to the action of bodies in the boiled extract which did not exist in the freshly expressed liquid.†

* See 'Annals of Botany,' vol. 2, p. 356 and figs. 55 and 56.

† De Bary inclined to the belief in a special ferment in the case of his *Peziza* (*loc. cit.*, pp. 418—420), but admitted that he had not proved the point either way.

The next question which arises is—Is there any definite body in the extract that could kill the protoplasm, and which would not be destroyed by the short boiling? The answer to this question is simple: the hyphæ of the fungus develop large quantities of oxalic acid* in the substratum, and this is a substance which is peculiarly poisonous to the living protoplasm of higher plants† if present in any large quantity. In the normal cells of plants rich in salts of oxalic acid (*Oxalis*, *Begonia*, &c.) I need only remind you that the acid is not in the protoplast, but is kept strictly isolated from it by the vacuole wall, as is clear from the researches of Pfeffer and De Vries.

It is at least conceivable, therefore, that the hyphæ kill the cells by flooding the protoplasm with oxalic acid; but it is not certain that they do not excrete a more subtle poison of the nature of a ferment.

In any case, it is a significant fact that the hyphæ kill the cells by emitting some soluble poison which causes the protoplasm to collapse, and then to turn brown, clearly because it destroys its power of retaining and restraining the sap in the sap-cavity; the latter therefore escapes through the now permeable dead or dying protoplasm, and owing to its acid contents, chromogenes, &c., stains it and the cell-walls brown as the oxygen of the air enters into combination.

There is thus, from the very first, a struggle between the hypha of the fungus and the cells of the host; the hypha is in the position of an attacking party, which has to overcome, first the outworks, in the shape of cuticle and cell-wall, and secondly the real fighting force—the protoplasm.

I take it that the attacking hypha (invigorated by previous culture, as said) excretes various zymase-like substances formed in its metabolism; one of these succeeds in overcoming the resistance afforded by the cuticle‡ and then the cell-wall is penetrated: the partially victorious hypha then advances in the cell-wall, and is nourished by the cellulose which it goes on dissolving, and under its changed conditions of life excretes in increasing quantities yet another zymase or some kind of poison which diffuses to the protoplasm. Now comes the real tug of war—so long as the outer layer of the protoplasm (the ectoplasm) is in a position to refuse access to, or in any way to destroy, the poison, the rest of the protoplast remains impermeable, and the hyphæ keep to the cell-

* De Bary observed the same in the case of *Peziza sclerotiorum* (*op. cit.*, pp. 399—403), and it is a common phenomenon in fungi. See, *e.g.*, Zopf (Schenk's 'Handb.,' vol. 4, 1889, p. 454).

† See de Vries, "Plasmolytische Studien über die Wand der Vacuolen" ('Pringsheim, Jahrb.,' vol. 16, 1885, pp. 565—6).

‡ Not impossibly, different zymases are concerned. See Wortmann ('Zeitsch. für Physiol. Chemi6,' vol. 6, 1882, pp. 287—329, especially pp. 321—329).

walls; but as soon as the protoplasm of a cell succumbs, it signifies its defeat by collapsing, and then its own more or less acid cell sap filters through to the walls and hyphæ. If this view is correct, and the evidence supports it entirely, it is clear that any variations in the host-plant which lead to weakening the outposts—cuticle and cell-wall—or diminishing the fighting power of the protoplast, increase the advantages of the hypha to a corresponding extent; and we have seen that such variations exist when circumstances cause the cells to become more watery and turgid, the cell-walls thinner and softer, and so forth. But, no doubt, the most important event is the lowering of the resisting power of the protoplasm, as must happen whenever external changes—such as low temperature, murky weather and a saturated atmosphere, &c.—combine in lessening the activity of respiration and assimilation, and consequently bring about the accumulation and possible filtration of organic acids, glucose, asparagin, &c.; for, in the first place, the lowered metabolism means less resisting power, no matter what hypothesis we adopt; and, secondly, the organic acids themselves prove an internal source of weakness if they become too abundant, and filter through the partially disorganised protoplasm. The protoplasm, then, has its powers diminished or destroyed by the accumulation and inhibitory action of products of its own activity.

Fortunately, however, we have something more than the above evidence, strong as it is, to support this view. Müller-Thurgau found, in the case of grapes devastated by *Botrytis cinerea*,* that the *Botrytis* mycelium lives on the sugar, acids, and soluble nitrogenous substances of the living cells; but he also discovered, by means of numerous comparative analyses, that the mycelium consumes especially the organic acids, the sugars to a less extent, and the soluble nitrogenous matters were all converted into insoluble nitrogenous substances.† No doubt some of the destruction of the acids is to be put down to direct oxidation, but much is due to assimilation by the fungus. Similar events were found to occur when the *Botrytis* was cultivated as a saprophyte on the juice of grapes.

It is, however, not difficult to give experimental proof of the accuracy of the statements that the entrance of the hypha into the cell is dependent on the condition of the protoplasm.

If the mycelium of one of these fungi is placed on an uninjured

* Thiel's 'Landwirthsch. Jahrb.,' 1888, pp. 83—160.

† *Penicillium* behaved very differently: it took the sugars in greater proportion than the acids, and left the juices more acid than before. *Botrytis*, on the other hand, left the juices less acid than before, and more concentrated owing to the evaporation of water from the injured grapes, and it is interesting to note that these diseased (so-called *edelfäule*) grapes yield the best and sweetest wines of the Rhine district.

living carrot, or turnip,* and the whole placed in a moist atmosphere, &c., the hyphæ do not at first enter the tissues as above described, but form a dense mycelium on the surface, and branches from this slowly penetrate into the interior, producing the symptoms referred to. If the carrot or turnip is first submerged for half a minute into boiling water, however, the hyphæ plunge into the outer cells (the protoplasm of which has been killed by the hot water) at once. These facts are easily explained when we recognise that the hot water causes plasmolysis of the cells, and escape of the sap into the intercellular spaces, cell-walls, &c.; in short, destroys the fighting power of the protoplasm against the hyphæ. Moreover, the latter are invigorated by their saprophytic nutrition, and are able to excrete such quantities of ferment that the still living cells deeper in the tissues are unable to withstand the attack.

Equally conclusive is the following experiment:—

A mature firm shoot of a Petunia was infected with the mycelium, and the hyphæ penetrated into the cortex about 1 cm., and then grew no further; evidently because the cell-walls were thick, and their protoplasm disposed of the poisonous zymase as fast as it reached them. When the infection was made on slightly etiolated, rapidly growing shoots, however, the fungus entered at once, and destroyed the entire shoot off-hand.† This is explained by the thinner, watery cell-walls, and the less vigorous protoplasm, more acid cell-sap, and so forth, of the latter offering less resistance to the zymases or poison execreted by the hyphæ.

Another excellent case is the following. During the very wet, cold, and dull weather of the summer of 1888, plants suffered a good deal from such diseases as we are discussing, and the white lily-buds were utterly destroyed in my neighbourhood by an epidemic of *Botrytis*,‡ aggravated by the low rate of transpiration, and consequently retarded respiration and metabolism, and the diminished assimilation leading to paucity of carbohydrates. The cell-walls were thin and watery, the sap unduly charged with acids, &c., and the protoplasm of the cells less capable of dealing with the poison emitted in larger and larger quantities by the hyphæ of the invading fungus.§ It was a very easy matter to directly infect the tissues of these lilies at the time mentioned, but considerably more difficult to do so when

* As a rule, roots are less acid than other organs, and inflorescences more so than leaves, which again are more acid than the stem (G. Krauss, 'Ueber die Wasservertheilung in der Pflanze, IV, Die Acidität d. Zellsaftes,' 1885; also Warburg, *loc. cit.* p. 116).

† De Bary, 'Bot. Zeitung,' 1886, col. 440—441.

‡ See 'Annals of Botany,' vol. 2, 1888, pp. 319—376.

§ Warburg showed that the leaves of *Lilium candidum* contain more acid when the temperature is lowered (*op. cit.*, p. 140).

the weather improved; and I have noticed the same fact in other cases as well.

Invigoration of Mycelium and Conidia by Saprophytic Mode of Life, and Differences in Behaviour of Successive Generations.

We have seen from the foregoing that the relations of the host to the parasite may depend very much on the condition of the former, as induced by the complex action of the environment. I have now to show you that the variations from a normal which culminate in an epidemic are not confined to the host; but that the parasite also exhibits phenomena leading to the same result.

That the mode of nutrition influences the vigour and size, &c., of a fungus is a fact well known; but it is a comparatively recent discovery that certain fungi, usually saprophytic in their habits, may be educated as it were to parasitism.* Thus, *Penicillium glaucum*, usually regarded as the type of a saprophyte, causes rotting in fruits, bulbs, &c., when its spores penetrate into a wound in the living organ;† and many other fungi usually met with as saprophytes are capable of assuming a parasitic mode of life if opportunity arises,‡ *e.g.*, species of *Mucor*, *Pythium*, *Nectria*, *Agaricus*, &c.

The most instructive of all is the genus *Botrytis*, however, for it is apparently possible to carry the process of "educating" this saprophyte to habits of parasitism much further than in any other cases known.

It was pointed out as early as 1874, by Zimmermann,§ that *Botrytis cinerea*, long known as a common saprophyte on fallen dead vine leaves, passes from the rotting *débris* on the ground to the healthy living leaves of several plants and develops spots on them; and the same fungus has been found as a parasite on the male inflorescences of junipers, thujas, and other Conifers,‖ as well as elsewhere. But a still better case than any of these is the occurrence of a severe epidemic on the gentians in the Jura during the wet summer of 1888.¶ The infection of the plants occurred in the young parts

* The converse is also true to a certain extent. See B. Meyer "Ueber die Entwicklung einiger parasitischen Pilze bei saprophytischer Ernährung" ('Landw. Jahrb.,' 1888, vol. 17); and Brefeld, 'Botan. Unters. ü. Hefenpilze,' Part V, 1883.

† See Sorauer, 'Pflanzenkrankheiten,' vol. 2, p. 92; Müller-Thurgau (*op. cit.*) says *Penicillium* causes a speckling of living grapes.

‡ See de Bary, 'Comp. Morph. and Biol. of the Fungi,' pp. 379—380.

§ "Ueber verschiedene Pflanzenkrankheiten" ('Hamburger Garten- und Blumenzeitung,' 1874).

‖ Klein, 'Verhandl. d. Zool.-Bot. Gesellsch. zu Wien' (vol. 20, p. 547), and Sorokin, 'Mykologische Skizzen' (Charkow, 1871).

¶ Kissling, 'Zur Biologie der *Botrytis cinerea*' (Dresden, 1889, p. 6). It is worth notice that this epidemic occurred in the same dull, cold, damp summer (1888) as the one on lilies in this country.

of the flowers, especially the stigmas and anthers, by means of spores. After growing outside the organs for some time, the hyphæ—now invigorated by their saprophytic nutrition—were able to enter other tissues, *e.g.*, those of the leaves, pedicels, &c. Experiments were then tried with *Echeveria metallica** with complete success, and it may be remarked that this disease is very common in a sporadic form on Crassulaceæ in green-houses. Infections of *Lilium* were also successful, and *Hemerocallis flava* was destroyed with extraordinary rapidity. Many other plants were also infected successfully.

In all these cases the spores only infected (directly) the most delicate or least protected parts of the flower, but the resulting mycelium when invigorated by its growth in the dead tissues was capable of directly infecting the ordinary tissues of plants.

It will be remembered that de Bary came to a similar result with his experiments,† and I have observed the same phenomenon over and over again with several of these forms. There is one, for instance, which sometimes cases great havoc among snowdrops in the early spring, and I found that the infection occurred especially by means of small invigorated mycelia developed from spores which germinated on the dead tissue of the sheaths at the base of the leaves; these hyphæ easily penetrated into the etiolated bases of the leaves and young flower-buds, especially when the plants were partially buried in snow.‡ Similarly with onions, hyacinths, and other plants; and similarly in every greenhouse on plants too far from the light, and often in store cellars on etiolated geraniums, calceolarias, and other plants put by for the winter.

But a still more remarkable proof of the influence of nutrition on the fungus is shown in the recent discovery that the conidia of successive generations of the *Botrytis* have different powers of infection.

It has already been pointed out that the conidia may or may not directly infect the tissues, and that one set of events affecting this is the condition of the tissues themselves: another, however, is the kind of food-materials on which the mycelium is growing which yields the conidia. I have found that if the attempt is made to infect a carrot with conidia taken directly from the *Botrytis* growing on artificial solutions it often fails, whereas the conidia produced on the carrot as a substratum succeed more easily; moreover, there was so much variability in the infections, and especially in the rate of progress of

* N.B.—This is one of the plants which is particularly rich in organic acids, and shows well the influence of warmth and daylight in diminishing them (see Warburg, *loc. cit.*, especially pp. 125, 132, 133, 134).

† 'Bot. Zeitg.,' 1886, col. 396 (see also the remark under *Sclerotinia Fuckeliana* in 'Comp. Morph. and Biol. of Fungi,' p. 380).

‡ A circumstance distinctly calculated to retard the decomposition of the acids and to bring about a tender etiolated condition.

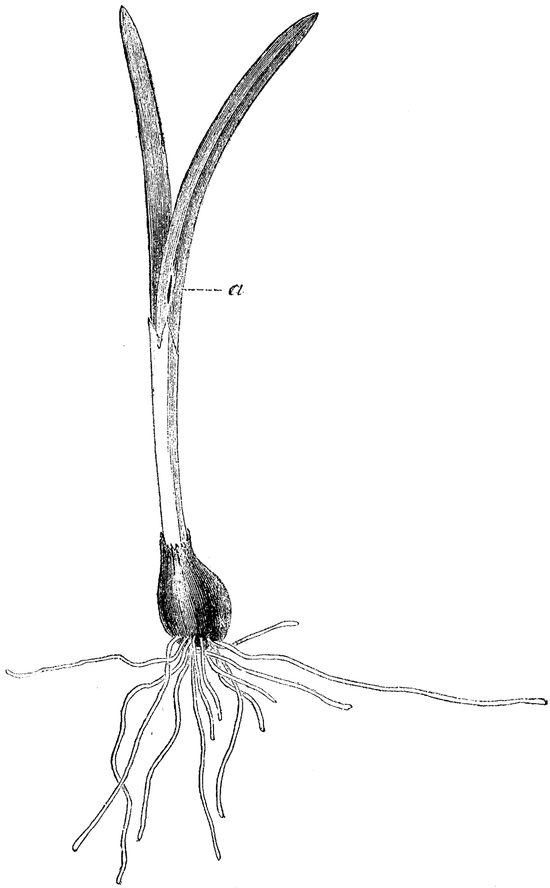

FIG. 11. A young snowdrop plant, artificially infected with *Botrytis.* The infection-spot (*a*) is sunken in the centre, and deep sienna brown or nearly black; the paler area around is yellowish-brown. The fungus hyphæ extend from this centre into the tissues, or not, according to circumstances. (See text.)

the infecting mycelium, that I was continually puzzled to account for the phenomena, and suspected that the conidia varied in infecting power, according to their size as well as the manner of culture. This would be a natural conclusion from what was already proved with regard to the invigoration of the mycelium, for, after all, conidia are only slightly specialised bits of mycelium cut off for purposes of rapid propagation,* and we may expect them to be directly affected by

* See Sachs, 'Lectures on Phys. of Plants,' p. 722; also de Bary's critical remarks in 'Comp. Morph. and Biol. of Fungi,' p. 129.

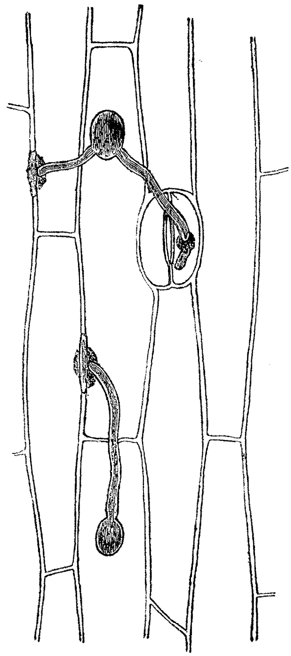

FIG. 12. Spores of *Botrytis* germinating on the epidermis of a snowdrop, and infecting it by means of their germinal tubes, the tips of which penetrate the cell-walls by means of secreted zymases, and cause them to turn brown at the points of entrance, as shown by the shading. (Highly magnified.)

everything which promotes or retards the vigour of the mycelium. I regard the conidium as distinct from any vegetative piece of mycelium chiefly in its capacity to form the necessary (cellulose-dissolving, &c.) ferment or zymase* in greater quantity or in a shorter time (with respect to the size of the organ), and look upon its size, shape, and colour, &c., as so many adaptations to the mode of life of the fungus.

Be this as it may, the conidia vary in infective power according to their nutrition—*i.e.*, according to the substratum on which the mycelium grows—and according to the generation to which the conidium belongs, *i.e.* (as I interpret it), according to the increasing vigour of the successive mycelia which produce the conidia.†

This latter fact is best demonstrated as follows: A crop of conidia is grown on a given pabulum, *e.g.*, on the moist sclerotium; the conidia are sown on the cut surface of ripe, sweet pears, and produce mycelia,

* See 'Annals of Botany,' vol. 2, 1888, p. 356.

† Kissling (*op. cit.*, p. 31) has proved this for *Botrytis cinerea*.

whence conidia again arise; these are again sown on pears, and produce a still more vigorous mycelium and crop of conidia, and so on. Calling the first crop of conidia generation I, and the second crop generation II, the third generation III, and so on, it was found that if the conidia of generation I are sown on similar leaves of a *Sempervivum* in a tiny drop of sap they do not infect the leaf; whereas those of generation II, similarly sown, infect the leaf at once, and those of generation III are still more virulent.

Kissling,* who has paid special attention to this point, and has carried the matter much further than other observers, measures the infective power of the conidia by the size of the disease-spot they produce in a given time.

As I have shown, the penetrating germinal hypha causes the cells in its neighbourhood to collapse and turn brown, because the excreted ferment or poison destroys the cellulose, and makes the protoplasm unable to retain the sap, which consequently suffuses and browns the area concerned. Now it is obvious that the rapidity with which this browning occurs may be taken as a rough measure of the progress—and, therefore, of the destroying power—of the infecting hyphæ, other things being equal. Well, Kissling took the necessary precautions, and set the conidia of succeeding generations I, II, and III to work on the surface of various fruits and other parts of plants, of course using the same substratum in any one series of experiments.

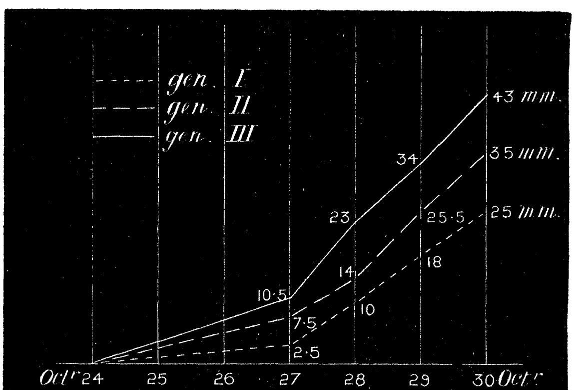

FIG. 13. Diagram constructed to show the relative progress of infections produced by successive generations of conidia of *Botrytis cinerea* (see text). The three different generations are denoted by differences in the characters of the curves. The horizontal base line is divided into six equal parts representing days; the distances measured on the ordinates represent the diameters of the disease-spots in millimetres, according to Kissling's experiments.

* *Loc. cit.*, pp. 22—29.

In a day or two the infected circular areas, as marked by the brown colour, were large enough to measure in millimetres, and by measurements on successive days he was able to judge of the progress of this extraordinary race, and he comes to the conclusion that on the same substratum the conidia vary, according to their generation, in their power of destroying the tissues. Those of the third generation, for instance, not only germinate more rapidly and vigorously—indications that they start in the race better equipped in the matter of food-materials and ferment-yielding substances—but they also destroy the cells of the host which they compete with more rapidly—which, no doubt, indicates that they are able to produce or manufacture more poison in the same time.

Summary of the Factors of an Epidemic—Bearing of the Discussion on other Parasitic Diseases—Conclusion.

It will be clear from the foregoing that in the case of an epidemic fungus disease, such as we have been considering, there are several classes of factors to be regarded, and I may sum up the chief points somewhat as follows. First, we have the normal healthy host-plant, with all its hereditary (internal) and adaptive peculiarities; secondly, we have the parasitic fungus, also with its disposition. Then we find, thirdly, that, apart from its inherent powers of variation, the host is subject to variable external influences during its life, which may produce such changes in the cell-walls and contents, &c., that the plant approaches nearer and nearer the limits of health, wide as we may regard these. On the other hand, we have, as a fourth consideration, the parasite also varying under the influence of changes in the factors of the environment, and its variations may, of course, be also dangerous to its welfare; but they may, on the contrary, be in such directions that it is enabled to profit by the counter-variations of the host. When the combined effects of the physical environment are unfavourable to the host, but not so or are even favourable to the parasite, we find the disease assuming a more or less pronounced epidemic character.

It is not pretended that we have here a totally new idea, because it has long been known that some organisms which bring about parasitic diseases do vary in the intensity of their effects, and can be made to do so artificially, and we know that some of the most brilliant results in biology have been obtained in connexion with certain lower organisms; but I have simply sought to show some of the links in the chain of causes and effects in the definite case of certain epidemic diseases of plants produced by the parasitism of some of the more highly developed fungi, and this, I think, has not been done before. If the preceding argument is admissible, new light will be thrown

not only on the cases of parasitism referred to, but also on the behaviour of the host in its struggle for existence with the factors of the inorganic environment, generally.

The question as to how far this view of the matter may be extended to other parasitic diseases of plants cannot be answered at present. Obviously the reflections excited will suggest lines of enquiry, and I may appropriately bring these remarks to a conclusion by a few brief comments on what is known as to the behaviour of other classes of parasitic fungi in this connexion.

Omitting the *Schizomycetes*, partly because they have a literature to themselves, and partly because they rarely* occur as parasites in the cells of plants, possibly owing to the acidity of the sap; and the *Myxomycetes*, of which Woronin's *Plasmodiophora*† is the best and most curious case; we have pronounced parasites (capable of producing epidemics) among the *Peronosporeæ*, one of which (*Phytophthora infestans*) has been more studied, probably, than any other true fungus parasite, at any rate so far as its life-history is concerned.‡

Much that has been stated in this lecture would, apparently, apply to the potato disease, and in view of the extreme interest that necessarily attaches to that malady, I draw attention to the following points of interest.

Suppose we take a potato plant the leaves of which are very slightly marked with minute disease spots, and divide it into two halves as exactly alike as possible, and place each half in a tumbler of water; the two tumblers, with their half-plants, are then placed in an ordinary room, side by side, at a temperature of about 20° C., and one is covered close with a bell-jar and the other left uncovered. In a short time—often a few hours—the covered leaves become black and rotten with the disease, whereas the uncovered one will go on looking fresh for several days, though it also succumbs at once if covered.§

The question arises whether the rapid spread of the fungus and the rot it causes here are simply owing to the increased supply of water, as the tissues become turgid in the saturated atmosphere under the bell-jar; or whether we have not here again, in addition, a case where the diminished access of oxygen to the interior of the tissues of the host results in an accumulation of organic acids and other substances which make the excessively turgid cells and thin, watery cell-walls more than usually easy prey to the parasite.

* Exceptions probably occur in the case of Wakker's hyacinth rot, the American "pear-blight," the "peach yellows," and a few others. See de Bary's 'Lectures on Bacteria,' 1887, p. 177, and the 'Reports of the U.S. Department of Agriculture,' especially No. 9, 1888.

† Pringsheim's 'Jahrb. f. wiss. Bot.' (1878, vol. 11, p. 548).

‡ See de Bary 'Morph. and Biology of the Fungi' for the chief literature.

§ See de Bary 'Die gegenwärtig herrschende Kartoffelkrankheit,' 1861, p. 55.

I ought to add, that if a potato plant is grown in a pot and kept under a bell-jar (untouched by *Phytophthora*) normally lighted, in the summer, the excessively watery dark-green shoots often develop hump-like outgrowths, composed of very large, thin-walled cells, which may be regarded as due to the excessive turgescence and hypertrophy of these cells. Presumably they contain relatively large quantities of organic acids, &c., and everything indicates that such a shoot would easily succumb to the *Phytophthora*, as in fact it does.

Kühn long ago noticed* that there are two periods when the potato shoot is most easily infected by the *Phytophthora*. The first is while still young—fully developed internodes are much more difficult to infect than young growing ones, a fact well known and easy to confirm; the second period is said by Kühn to occur after the tissues are far advanced, at the end of July or the beginning of August, and this would seem to be borne out by the experience of cultivators generally. I am inclined to regard this second period as coincident with the time when the plant is particularly rich in the products of assimilation on their way down to the tubers. They travel chiefly as glucose, and one consequence of the abundance of this carbohydrate, and the increased metabolism it supports, is an increase in the organic acids. If wet and dull weather sets in when the tissues are thus, so to speak, overflowing with such substances, the *Phytophthora* is peculiarly favoured, and can spread through the plant with the rapidity characteristic of an epidemic. In the allied genus *Pythium*, the phenomena are so similar that we may assume that the fungus behaves like Peronospora: the species are often saprophytes, however.

The question now arises, can these ideas be extended to the case of other parasitic fungi? It would be difficult to say with regard to the *Saprolegnieæ* and the *Mucorini*, because so little is known of their parasitism. As regards the *Ascomycetes* generally, we may expect great differences in respect to types like the *Gymnoasceæ*, *Rhytisma*, *Hysterium*, the *Erysipheæ* and the *Sphærias*, and they certainly occur.

Some *Nectrias* at any rate (†*e.g.*, *N. cucurbitula*, *N. cinnabarina*, and *N. ditissima*) behave so differently towards the host that we may probably conclude that the mode of procedure is unaffected by such variations on the part of the latter as have been sketched; and the same may be said of the wood-destroying *Hymenomycetes* (*e.g.*, *Agaricus melleus*, *Trametes radiciperda*, *Polyporus sulphureus*, &c.).

In all these cases the tree, as a whole, suffers in an indirect manner: these various cankers and rots, &c., destroy, for the most

* 'Ber. aus dem Physiol. Lab. u. d. Versuchsanstalt des Landw. Instituts d. Univ. Halle,' 1872, pp. 81—82, quoted by Sorauer, vol. 1, p. 140.

† 'Unters. a. d. Forstbot. Inst. zu München,' vol. 1, pp. 88 and 109, and vol. 3 also R. Göthe (Thiel's 'Landw. Jahrb.,' 1880, vol. 9, p. 837).

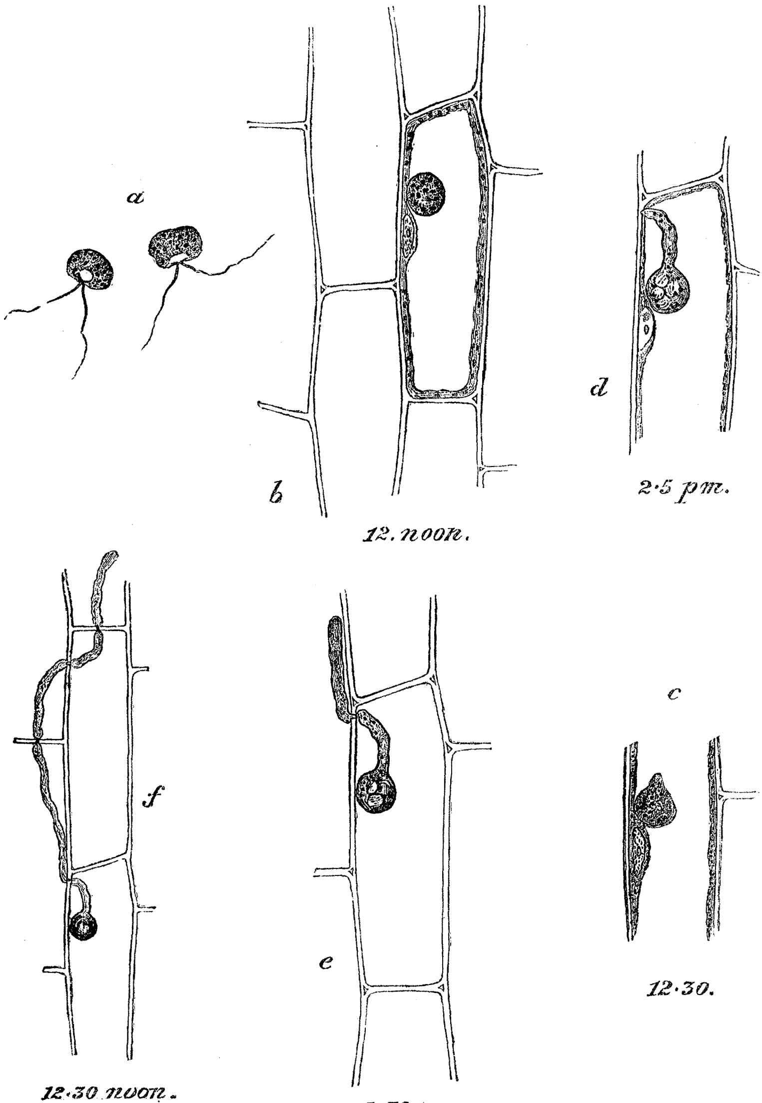

FIG. 14. Zoospores of a species of *Pythium* allowed to germinate in water on a piece of a longitudinal section of a bean-stem. The zoospores (*a*) soon come to rest, and one was noticed at mid-day on an exposed cell (*b*), lying nearly over its nucleus. At 12.30 this spore had begun to germinate and enter the cell (*c*). At 2.5 p.m. the germinal hypha had turned to the left, and commenced to bore through the side-wall with its tip (*d*). At *e* is shown the progress by 5.30 p.m. on the same day; and at *f* (smaller scale) the condition of affairs at 12.30 next day. That these hyphæ pierce the walls by means of secreted zymases can scarcely be doubted after what has been proved for *Botrytis*.

part, structures which are already dead, and so interfere with the transpiration current, and other large groups of functions, more by the mechanical injury done than by direct injury to living cells.*

In the group of the *Ustilagineæ* we have some of the most remarkable parasites known, and the relation of the host-plants (chiefly species of Gramineæ and Cyperaceæ) to them must be very different in detail.

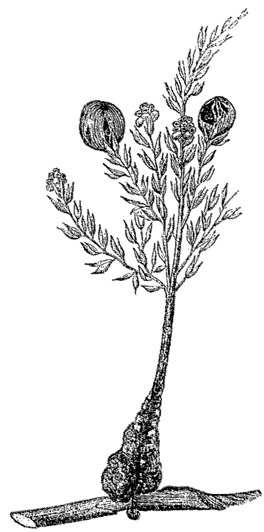

FIG. 15. *Zea mais.* Portion of inflorescence (reduced) with malformations produced by the parasitism of the fungus *Ustilago Maidis* (Sorauer).

In the more typical cases we find that the sporidia or conidia germinate in artificial nutritive media, and go on producing generation after generation of their like,† and this undoubtedly occurs in the open fields, &c. Brefeld states that he has cultivated one form through more than a hundred successive cultures in the course of a whole year, and that this corresponds to about 1500 successive sprout-series or generations,‡ but towards the end of the period the *germinating* power of the successive conidia became weaker and weaker, and at last failed.

* The germinal hyphæ developed from the spores of such fungi often find their way into the wood, cambium, &c., by means of wounds, caused by mechanical breakage, the nibbling of mice, squirrels, the punctures of insects, frost-cracks, the blows of hailstones, and so forth, which introduce us to a different aspect of the relations between host and parasite.

† Brefeld, 'Bot. Unters. über Hefenpilze,' part 5, Leipzig, 1883.

‡ Brefeld, in a lecture before the *Klub der Landwirthe zu Berlin*, 1888 ('Nachrichten aus d. Klub d. Landw. zu Berlin,' 1888, Nos. 220—222).

He also found that the conidia germinate, by developing a germinal tube only at a given period, and not at any indefinite time they may happen to be sown: consequently they are unable to infect the host unless they happen to be on the proper spot at the right time.

Now Kühn showed long ago* that the infection of the cereal by *Ustilago* can only occur near the "collar" of the young germinating seedling, and although differences have arisen† as to the exact spot in this region which alone can be infected, there is one point on which all are agreed, namely, that the germinal tube can only enter the young actively growing tissues in that region. Immediately the first internode is completed, the seedling is proof against infection in the open.‡

That it is really a matter of the age and condition of the tissue is beautifully demonstrated by Brefeld, who showed that if the conidia are forced into the bud by means of a syringe, so that they can germinate in contact with the embryonic cells at the growing point, infection may be ensured at any time.

But far the most interesting point about these fungi is that when the germinal hypha is once inside the tissues it goes on growing with them, keeping between the cells. Although we have almost no information as to details here, it can hardly be doubted that the chief agent in maintaining the balance of position in this case is the living substance in the cells of the host; but I know of no explanation for this beyond the general one, that so long as the cells of the internodes are actively performing their normal functions, the hyphæ have to be contented, so to speak, with a sort of suppressed existence in the intercellular spaces and middle lamella of the walls.

True, when the young fruits begin to fill out, the mycelium accomplishes a sharp revenge by destroying the whole fruit; but it is obvious that the relations which determine the epidemic or sporadic character of the disease are those between the tissues and the germinal hyphæ and young mycelium, and there are great variations in these matters, even in the group of the *Ustilagineæ* itself.§

Very different again must be the relations in detail between host and parasite in the case of those *Uredineæ* which cause epidemic leaf diseases, especially those which form haustoria,|| and it is almost impossible

* 'Krankh. d. Kulturpflanzen,' 1859, p. 46.

† *Cf.* Wolff, 'Brand des Getreides,' Halle, 1874; Hoffmann, 'Bot. Unters.,' 1866; 'Ueber den Flugbrand,' p. 206; Kühn, "Beobachtungen ü. d. Steinbrand d. Weizens" ('Oesterr. Landw. Wochenschr.,' 1880).

‡ This no doubt explains the fact that in a wet spring nearly all seeds with spores attached become infected, because the tissues remain in a youthful condition longer than in a dry season.

§ *E.g.*, contrast the behaviour of *Protomyces*, *Entyloma*, and *Ustilago Maidis*, for instance, with that of most other *Ustilagineæ*.

|| In all cases where haustoria are developed the mycelium enters into a peculiar

to say anything about their nutrition beyond the general statement that they must have established such close temporary relations with the living cells of the host that their protoplasm and that of the host can go on absorbing nutriment from the same sources. This would seem to be proved by the curious phenomena of hypertrophy which they induce, *e.g.*, the young shoots of *Euphorbia cyparissias* are entirely altered in habit by the *Æcidium* of *Uromyces Pisi*, and the well-known "witches' brooms" of the silver fir,* for although the changes induced

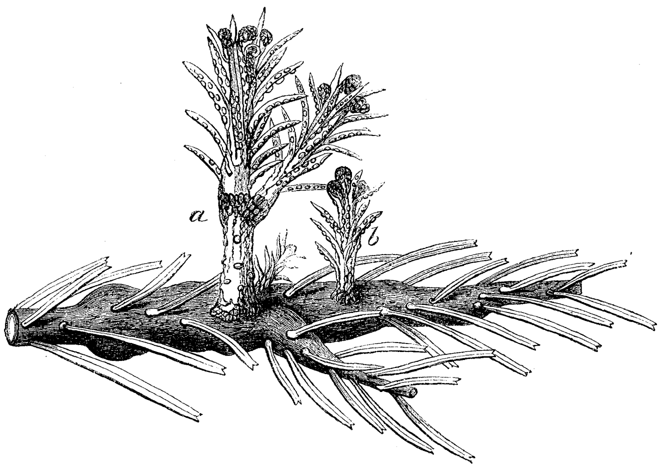

Fig. 16. A specimen of "witches' broom," on the silver fir, caused by the stimulating action of the Uredinous fungus *Æcidium elatinum*, the mycelium of which lives perennially in the cortex, &c., of the fir, and causes some of its buds to grow up into erect shoots of totally different habit from the normal branches. The blister-like Æcidia are visible on the leaves at *a* and *b* (Hartig).

imply that the cells are carrying out their functions in a modified manner, still they grow, divide, and evidently discharge their main duties much as usual. Consequently it is impossible to believe that any individual cell suffers much direct injury, and at least the protoplasm and nucleus, and even the chlorophyll corpuscles, &c., may re-

symbiotic connexion with the cells, and for some time merely taxes them, as it were, rather than injures them directly. Of course, there is ultimate injury, and even death, brought about in these cases; but how much this differs in different cases is evident from comparison of other fungi, like *Peronospora parasitica*, *Podosphæra Castagnei*, with Uredines such as *Hemileia vastatrix*, *Melampsora Goeppertiana*, &c.

* Such hypertrophies are not confined to the Uredineæ, however: *cf.*, de Bary, 'Morph. and Biol. of Fungi,' 368—369, and Zopf (Schenk, 'Handb.,' vol. 4, 1889 pp. 504—507).

main intact for weeks or months. No doubt in these cases also the entrance of the hyphæ or haustoria into the tissues is aided by any factors which cause the cell-walls to be softer or thinner than in the normal condition; and it is certain that many failures by those who have experimented with Uredinous fungi are attributable to their sowing the spores on older, well matured tissues.

We are here, however, abandoning the subject of the present lecture, because, in the first place, the phenomena just referred to appertain to sporadic rather than epidemic diseases, and because, secondly, they tend to the subject of *symbiosis* proper, where the relations between the host and the parasite have become so arranged that both may be said to benefit by the commensalism, as exemplified in the lichens, and some of the recently described cases of mutualism between fungi and the roots of Phanerogams.

April 17, 1890.

Sir G. GABRIEL STOKES, Bart., President, in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

The following Papers were read:—

I. "Preliminary Note on Supplementary Magnetic Surveys of Special Districts in the British Isles." By A. W. RÜCKER, M.A., F.R.S., and T. E. THORPE, Ph.D., B.Sc. (Vict.), F.R.S. Received March 5, 1890.

During the summer of 1889 we carried out additional magnetic surveys of the Western Isles and the West Coast of Scotland, and of a tract of country in Yorkshire and Lincolnshire.

Both districts were selected with special objects in view. We had found that powerful horizontal disturbing forces acted westwards from the Sound of Islay, from Iona, and from Tiree, and we had deduced a similar direction for the disturbing force at Glenmorven from Mr. Welsh's survey of Scotland in 1857–58. The whole district presents peculiar difficulties, partly from the fact that local disturbance is likely to mask the effects of the regional forces, partly because the normal values of the elements must be especially uncertain at stations on the edge of the area of our survey.

If, then, the general westward tendency of the horizontal disturb-

FIG. 2. Oaks in the neighbourhood of a manufacturing town, the leaves of which were damaged by acid gases. The injury results in the production of yellow spots on the leaves, and the latter eventually turn wholly yellow and brown, and die. From a photograph taken August 8th, 1882.

FIG. 3. The same oaks as those of fig. 2, photographed from the same spot on July 20th, 1888. The cumulative injury to the leaves in successive years results in the death of the trees.

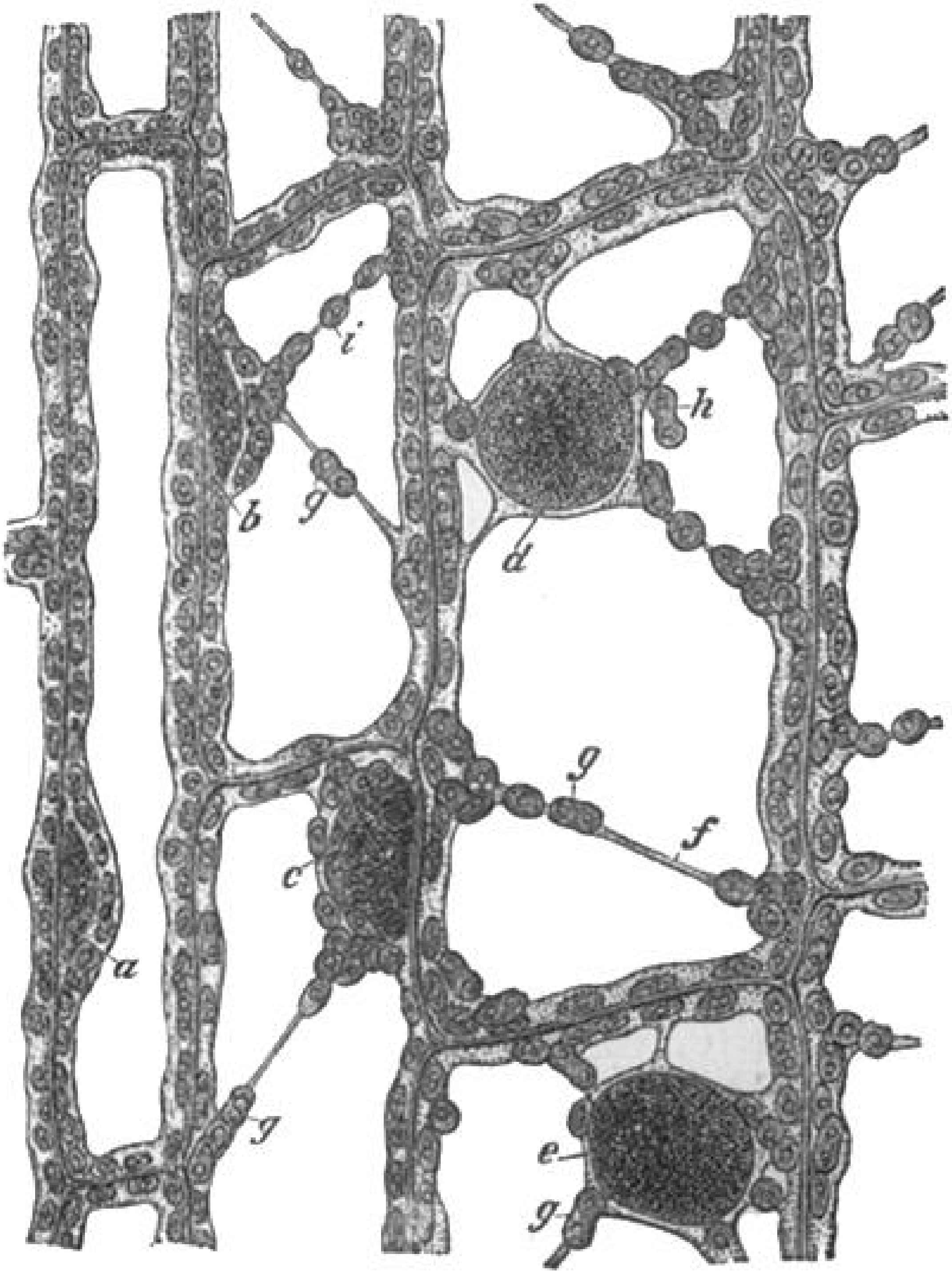

FIG. 4. Portion of the cell-tissue of a higher plant, in longitudinal section and highly magnified. Each of the cells is bounded by the cellulose cell-wall; and this is lined by the protoplasm in which are embedded the nucleus (*a—e*) and the green chlorophyll corpuscles (*g—i*). This protoplasm encloses the cell-sap, and strands of the former may pass across (as at *f*), or plates of protoplasm may separate the sap of one part of the cell from that of another (Kny).

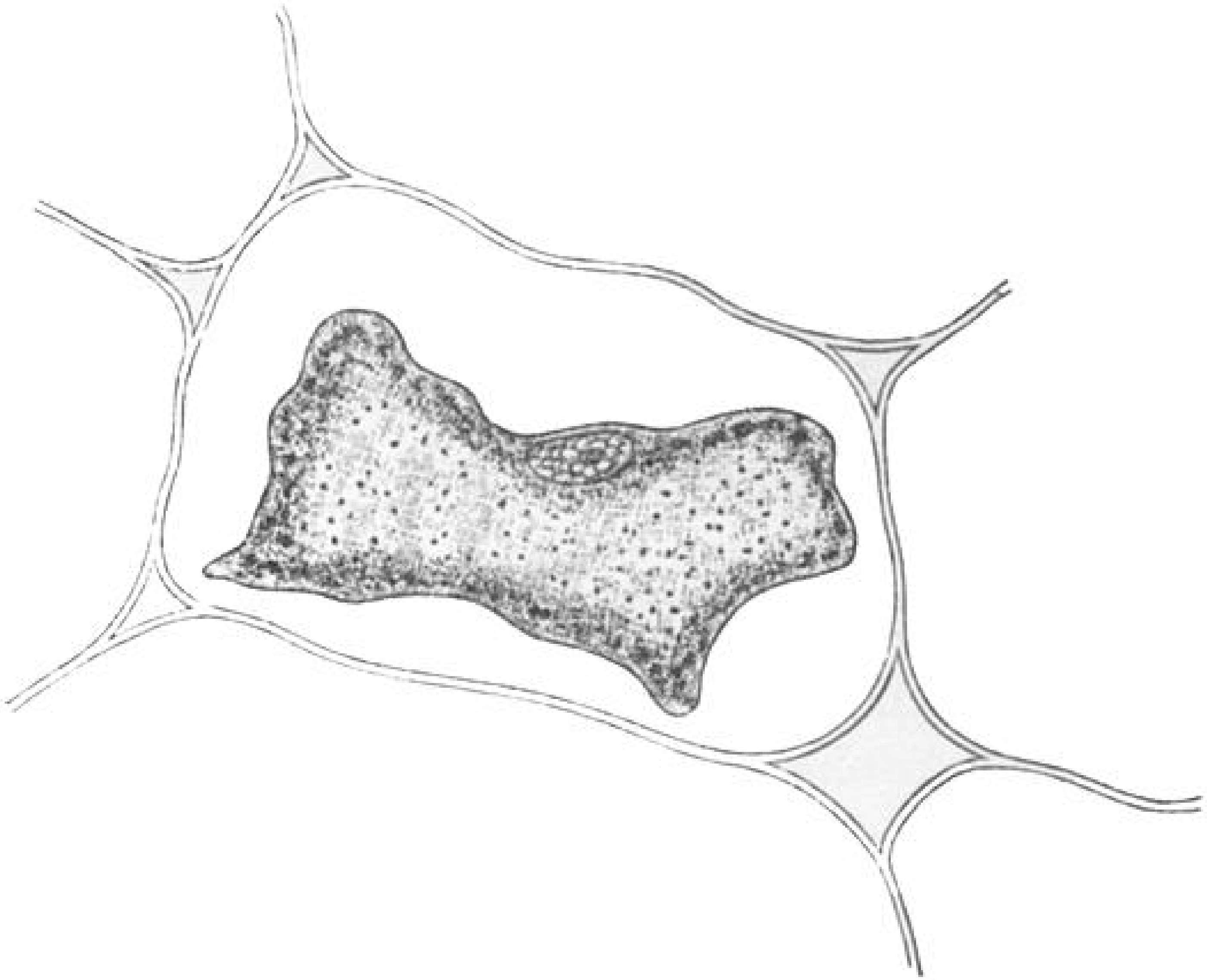

FIG. 5. A thin-walled parenchymatous cell killed by a few seconds' immersion in water at 75° C. The protoplast contracts from the cell-wall, carrying with it the nucleus and chlorophyll-corpuscles, and allowing the cell-sap to escape; the thin cellulose wall consequently becomes lax, and suffused with cell-sap. A similar result is brought about by longer immersion in water at lower temperatures (above 50° C.), or by very low temperatures, the action of poisons, &c. (Highly magnified.)

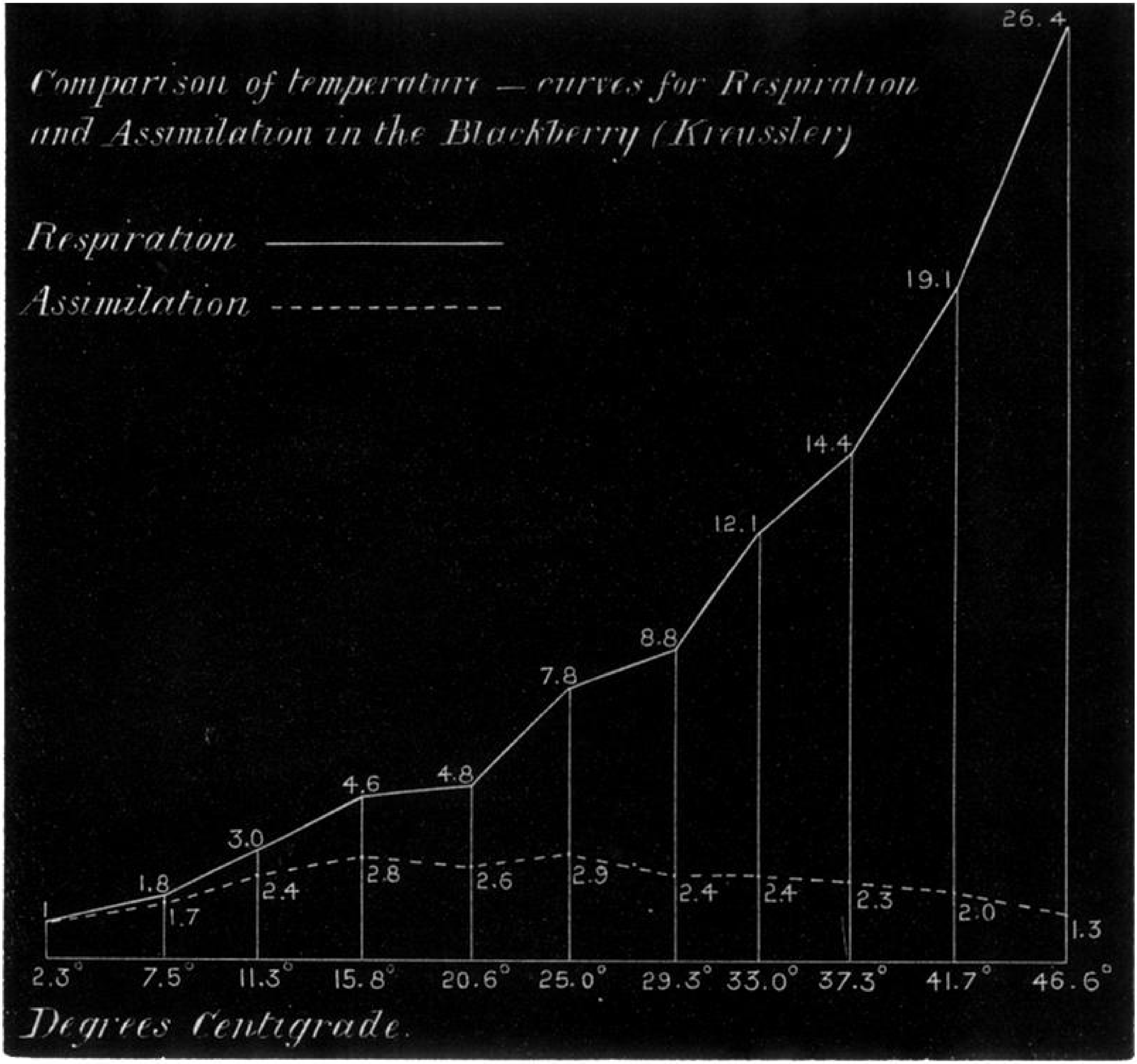

FIG. 6. Diagram constructed to show the comparative effects of equal increments of temperature on respiration and assimilation respectively, according to Kreussler's data. The base line has marked off on it a number of intervals corresponding to so many degrees centigrade, as denoted by the figures; on the ordinates from these points are measured distances corresponding to Kreussler's figures—numbers representing the comparative intensity of the functions in question, if that at the lowest observed temperature is taken as unity.

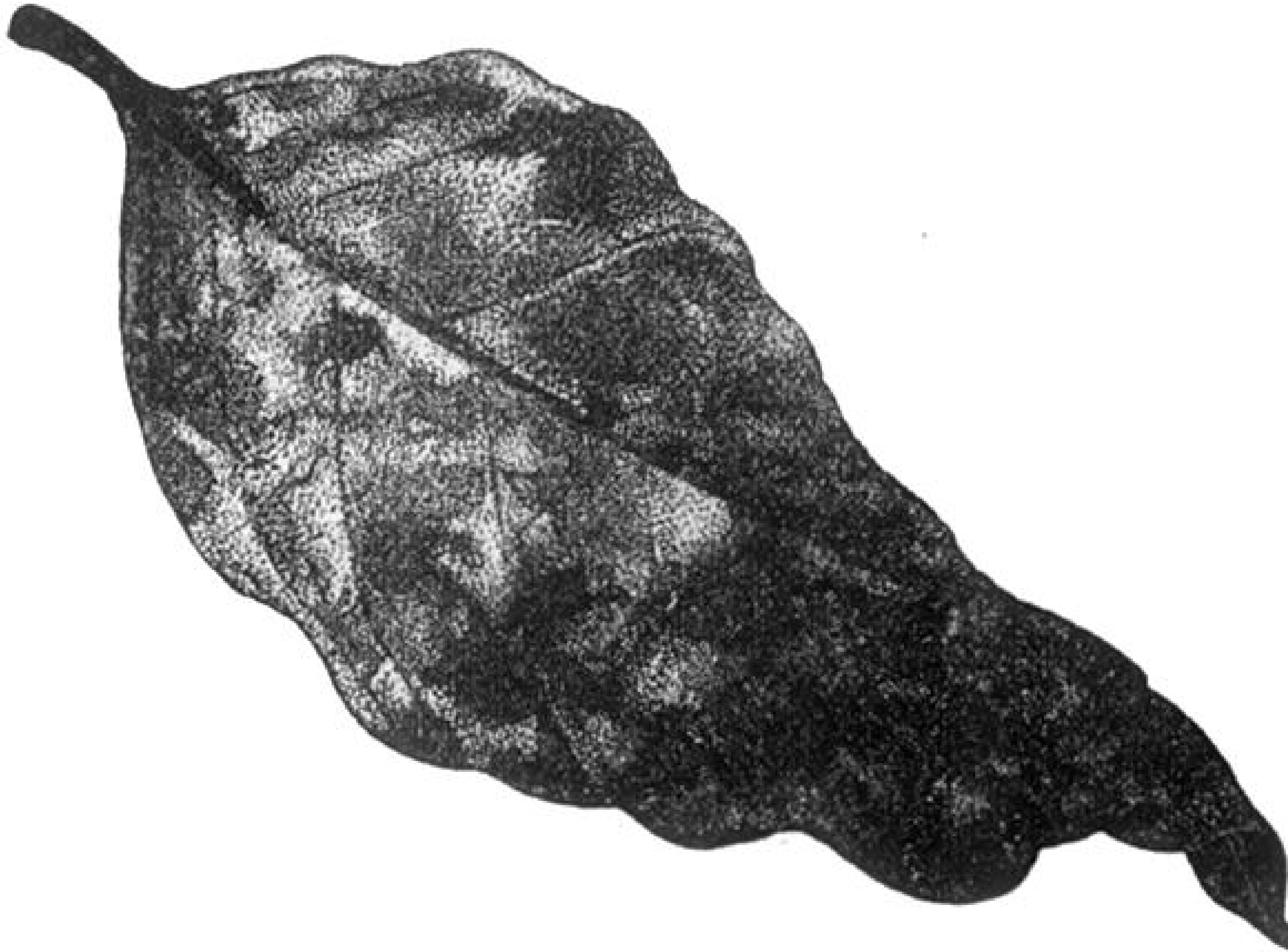

FIG. 7. A dead leaf infested with moulds, especially with *Botrytis*, as shown on the grey patches. (Natural size.)

FIG. 8. A bunch of "mouldy" grapes infested with *Botrytis cinerea*. The ravages of the fungus cause the skin to rupture, and the fruits to shrivel from loss of water; other changes in the substance of the contents are referred to in the text. Patches of the conidiophores are seen on the exterior (Müller-Thurgau).

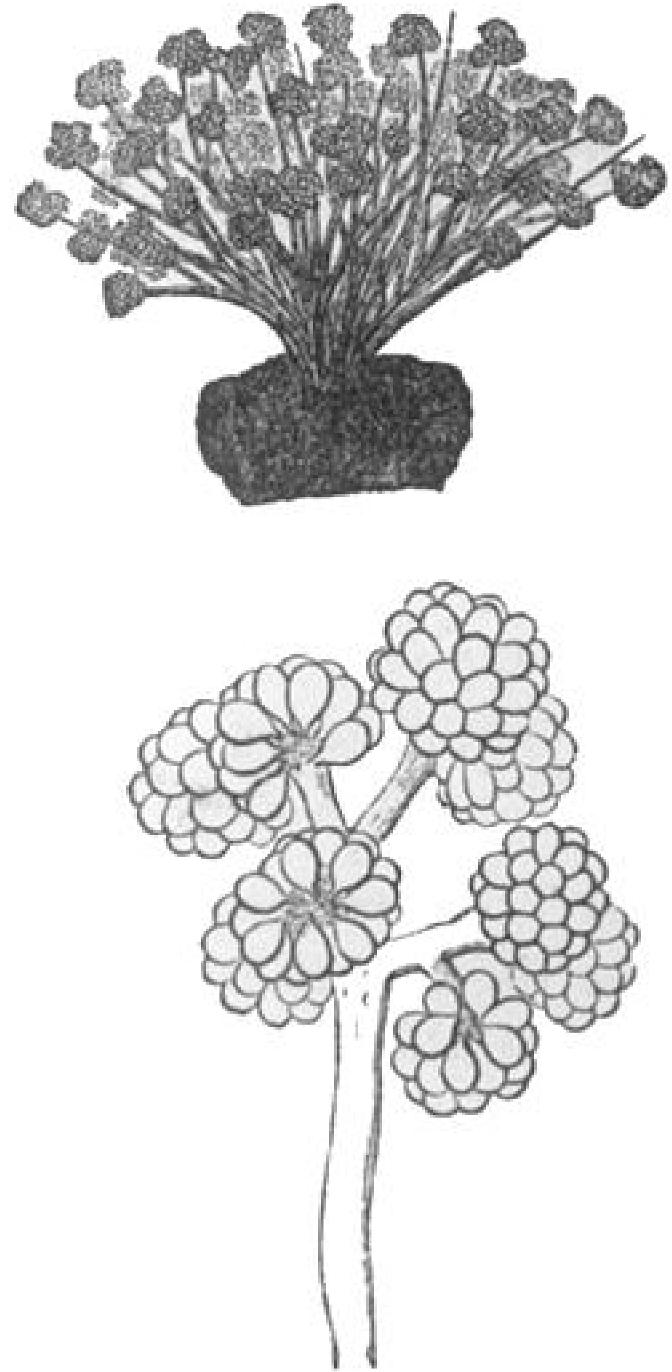

FIG. 9. *Botrytis cinerea.* The upper figure represents a tuft of the conidiophores breaking through the epidermis of a grape (magnified); the lower one is one of the conidiophores still more highly magnified.

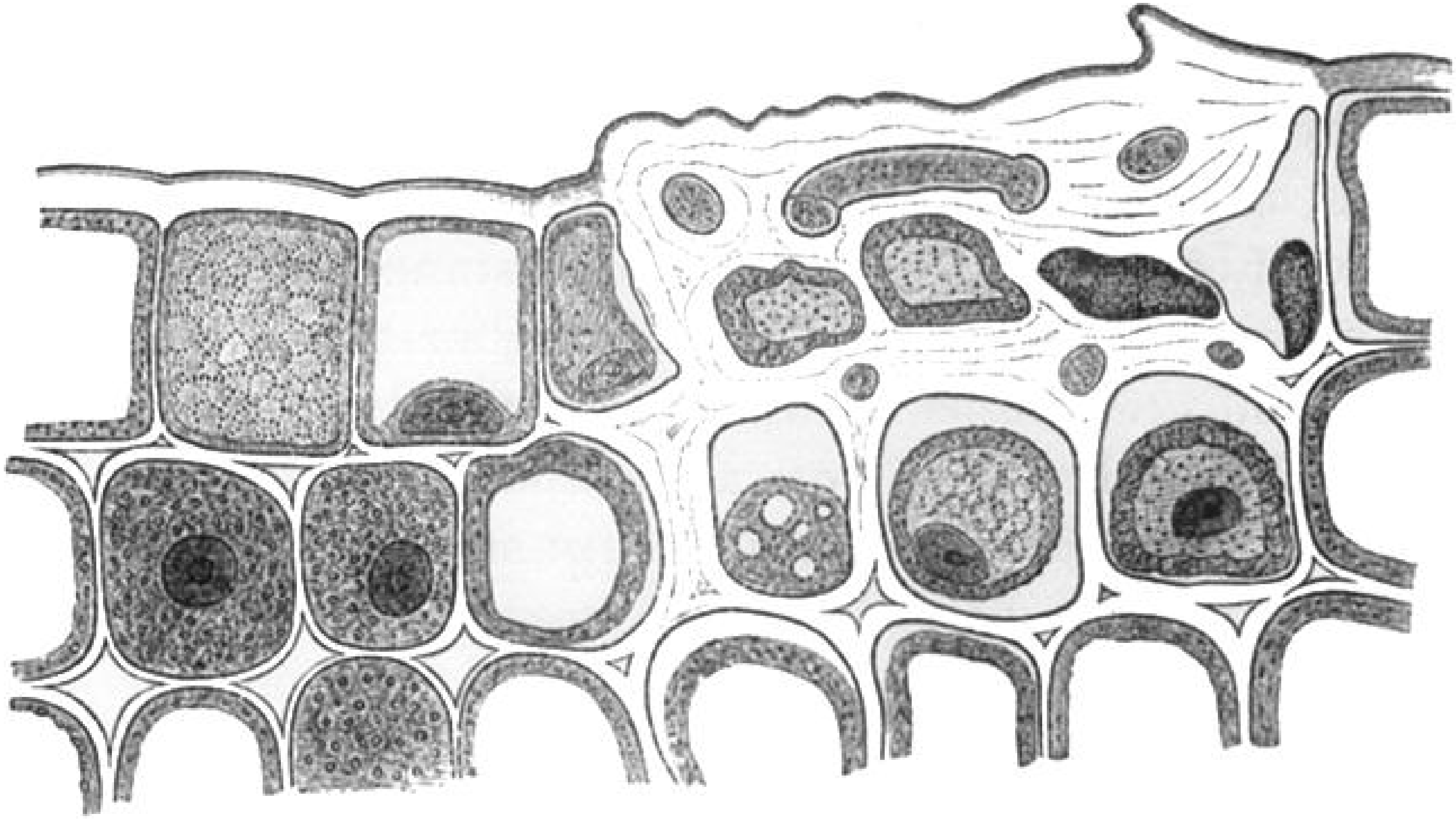

FIG. 10. Portion of a transverse section through an infection-spot in the tissues of snowdrop (such as that at *a* in fig. 11), showing the swollen cell-walls with hyphæ of *Botrytis* in them. The cell-contents also show changes; the protoplasm contracts, dies, and turns brown, and stains less and less readily the further the changes proceed; the cell-sap escapes and suffuses the cell-walls; the nucleus is the last to succumb. The above changes are exhibited by cells some distance away from the hyphæ, and are the less pronounced the further away the cells are. The colour reactions are of course not reproduced. (Very highly magnified.)

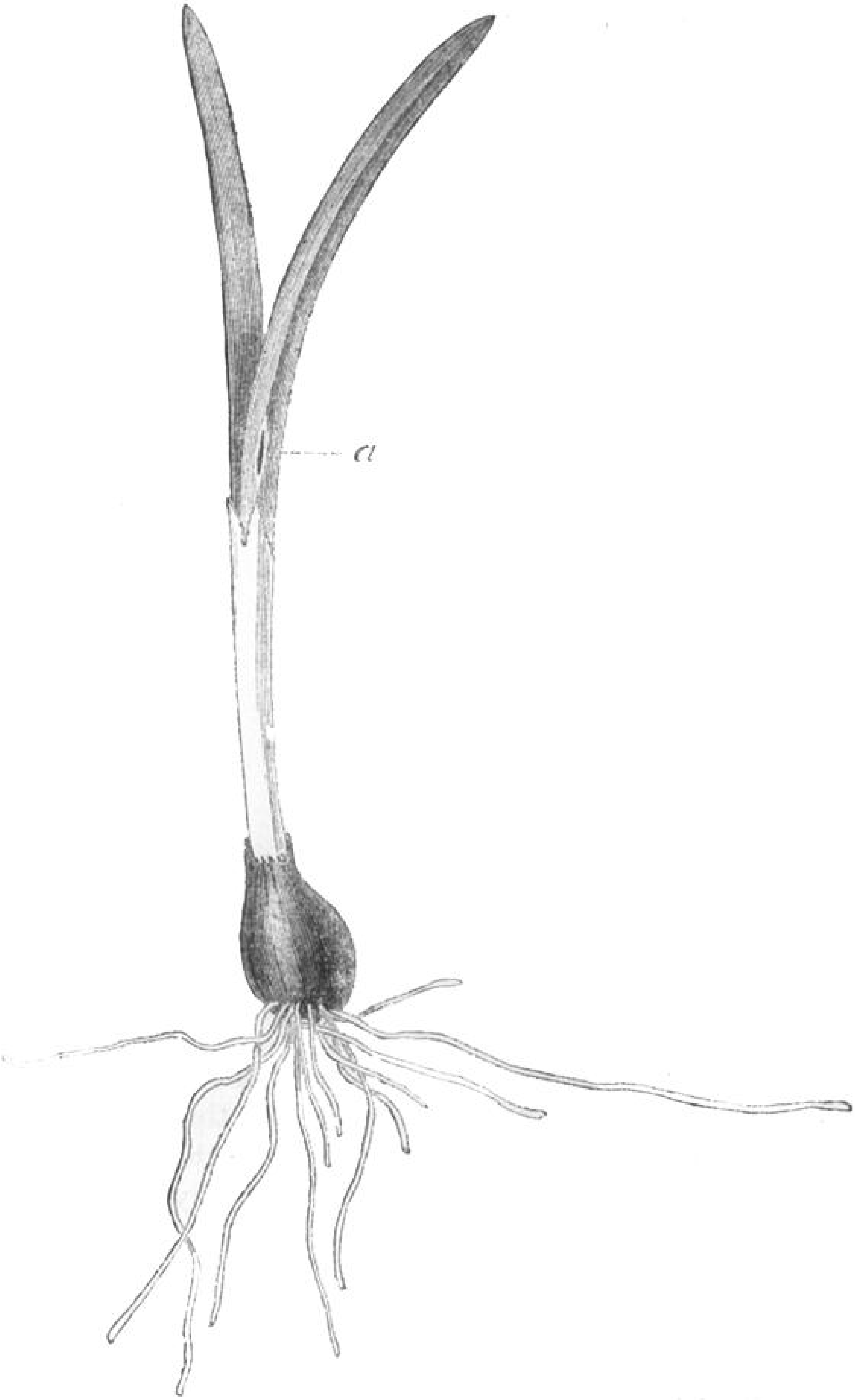

FIG. 11. A young snowdrop plant, artificially infected with *Botrytis*. The infection-spot (*a*) is sunken in the centre, and deep sienna brown or nearly black; the paler area around is yellowish-brown. The fungus hyphæ extend from this centre into the tissues, or not, according to circumstances. (See text.)

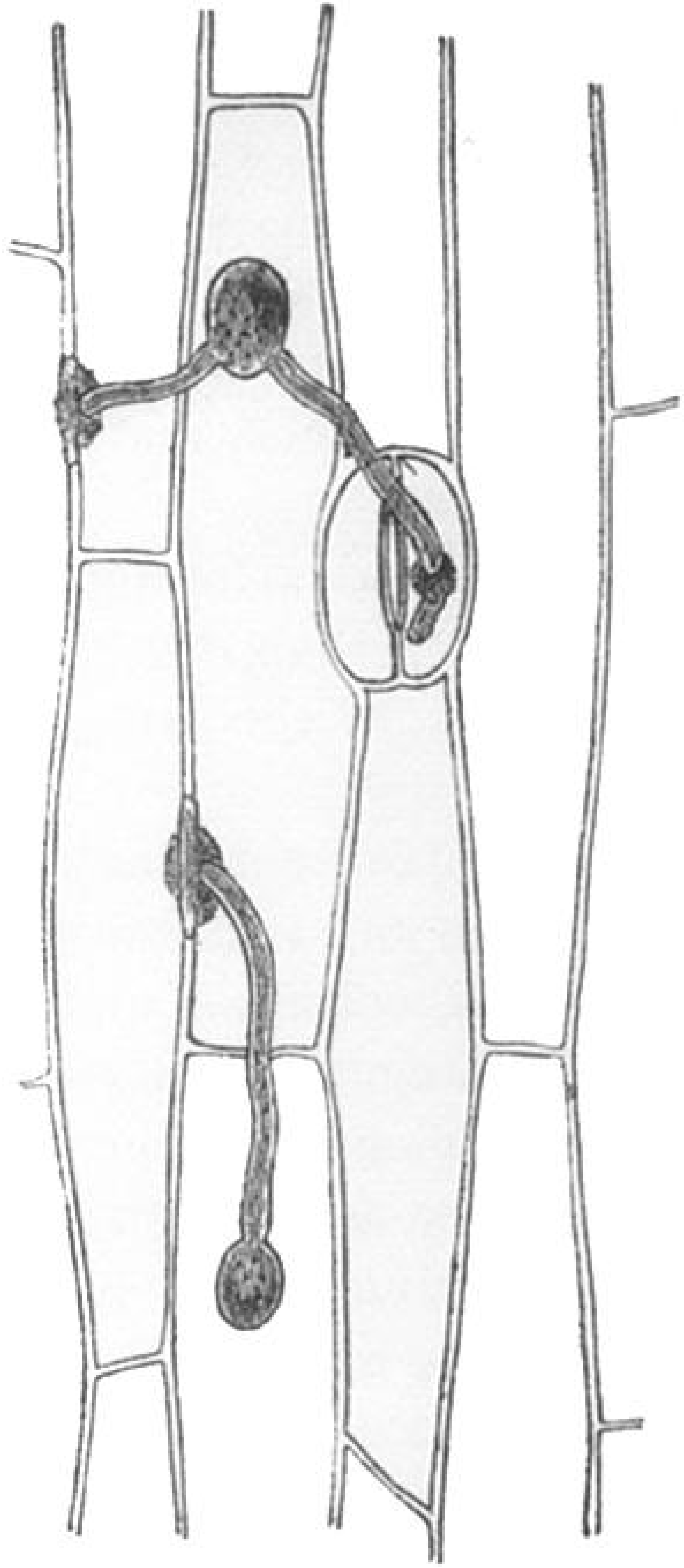

FIG. 12. Spores of *Botrytis* germinating on the epidermis of a snowdrop, and infecting it by means of their germinal tubes, the tips of which penetrate the cell-walls by means of secreted zymases, and cause them to turn brown at the points of entrance, as shown by the shading. (Highly magnified.)

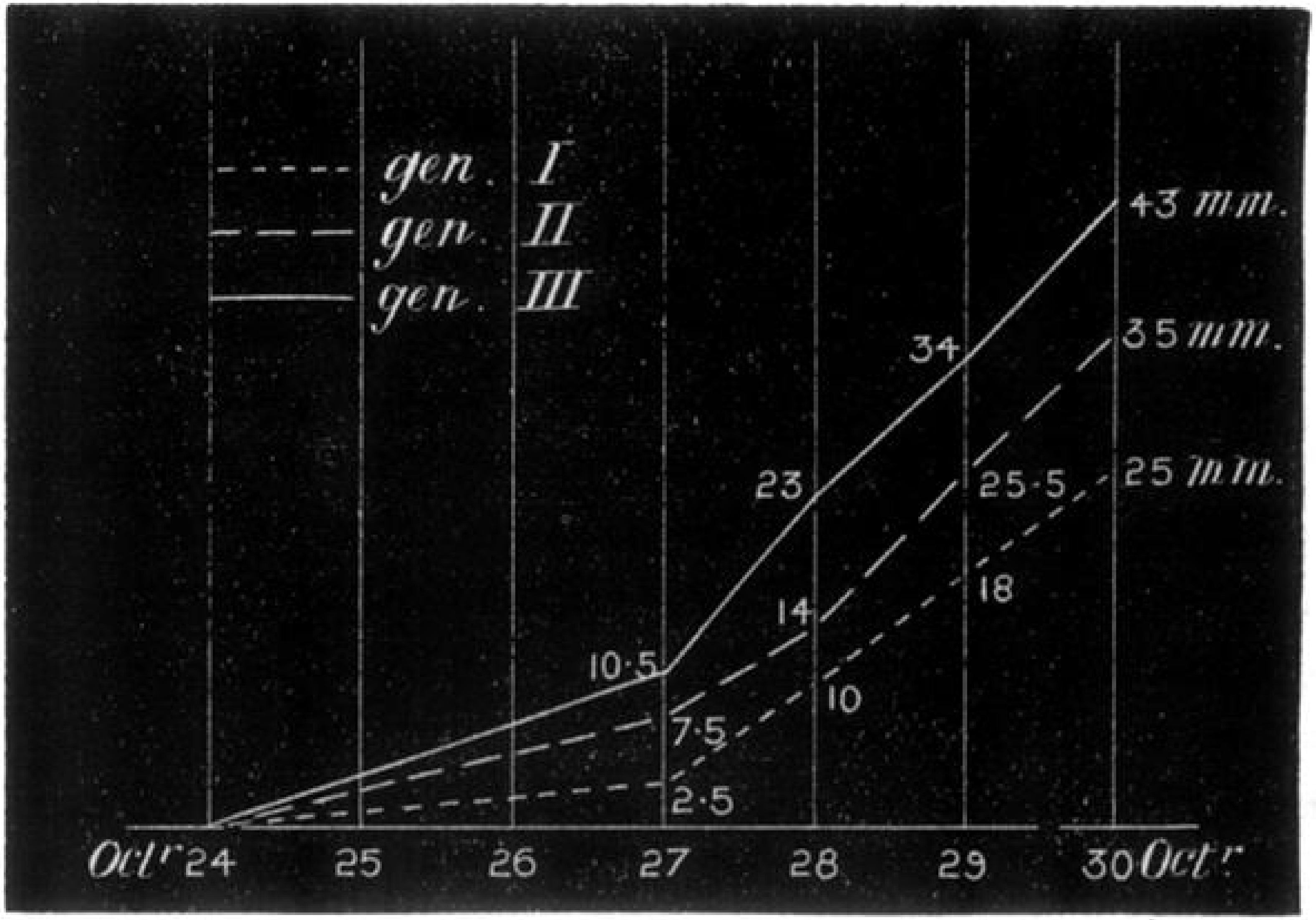

Fig. 13. Diagram constructed to show the relative progress of infections produced by successive generations of conidia of *Botrytis cinerea* (see text). The three different generations are denoted by differences in the characters of the curves. The horizontal base line is divided into six equal parts representing days; the distances measured on the ordinates represent the diameters of the disease-spots in millimetres, according to Kissling's experiments.

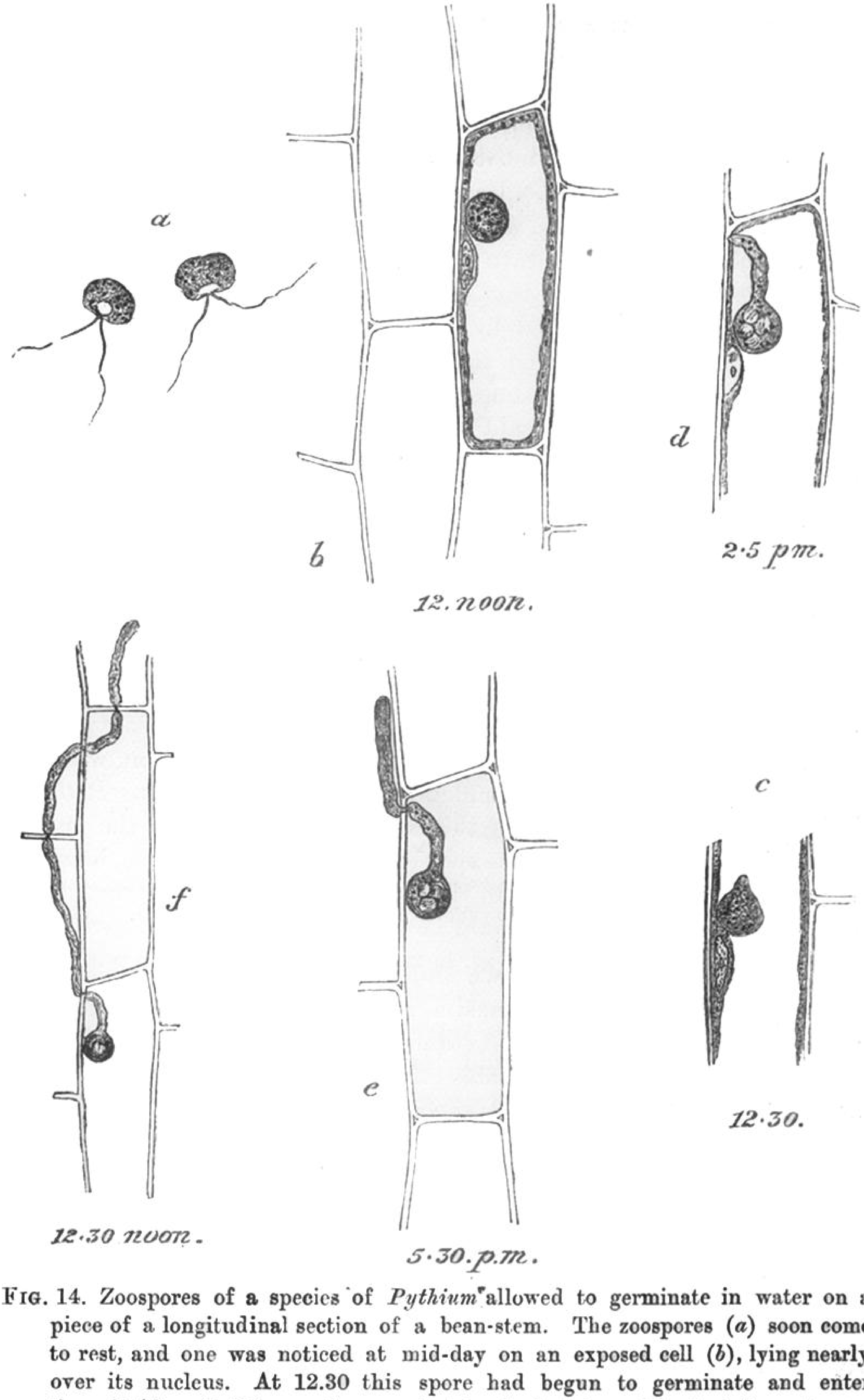

FIG. 14. Zoospores of a species of *Pythium* allowed to germinate in water on a piece of a longitudinal section of a bean-stem. The zoospores (*a*) soon come to rest, and one was noticed at mid-day on an exposed cell (*b*), lying nearly over its nucleus. At 12.30 this spore had begun to germinate and enter the cell (*c*). At 2.5 p.m. the germinal hypha had turned to the left, and commenced to bore through the side-wall with its tip (*d*). At *e* is shown the progress by 5.30 p.m. on the same day; and at *f* (smaller scale) the condition of affairs at 12.30 next day. That these hyphæ pierce the walls by means of secreted zymases can scarcely be doubted after what has been proved for *Botrytis*.

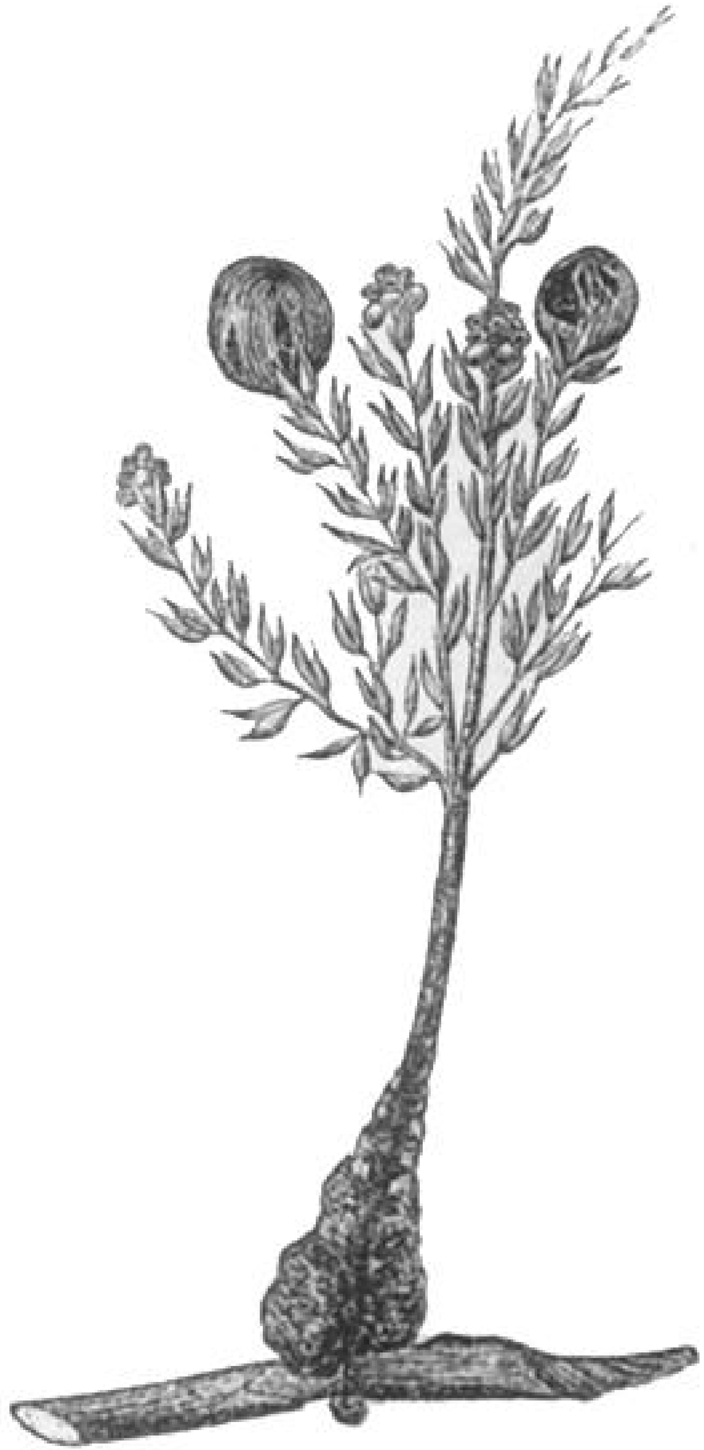

FIG. 15. *Zea mais.* Portion of inflorescence (reduced) with malformations produced by the parasitism of the fungus *Ustilago Maidis* (Sorauer).

FIG. 16. A specimen of "witches' broom," on the silver fir, caused by the stimulating action of the Uredinous fungus *Æcidium elatinum*, the mycelium of which lives perennially in the cortex, &c., of the fir, and causes some of its buds to grow up into erect shoots of totally different habit from the normal branches. The blister-like Æcidia are visible on the leaves at *a* and *b* (Hartig).