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Relations of Parasitic Fungi
To their Host Plants

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RELATIONS OF PARASITIC FUNGI TO
THEIR HOST PLANTS

BY

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Ernest Shaw Reynolds

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RELATIONS OF PARASITIC FUNGI TO THEIR HOST PLANTS

I. STUDIES OF PARASITISED LEAF-TISSUE

Various phases of pathologic study have occupied the attention of botanists at different times. Before the exciting causes of disease in plants were known, the general external appearance of the affected organ was described. Later, most of the attention was directed toward the discovery of the parasitic organisms which cause the derangements, and incidentally the study of the physiologic responses of the host was begun. Within the last few years many students of the subject have examined various morphologic changes which occur in diseased plants, first dealing almost entirely with the gross anatomical appearance, but later making more minute histologic and cytologic investigations. Leaf tissue, when invaded by fungi, however, has not been thus carefully studied. Moreover, comparative studies are always helpful in deciding general principles, and so it is in pathologic morphology. Only as we become acquainted with many examples of cytologic and histologic changes, shall we be able to approximate the truth regarding the reaction of the host plant to parasitic invasion. The practical value of such results can hardly be doubted. Mr. A. F. Wood(92)

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(92) Science (1907) p. 554.

 

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has written of this matter as follows: "To most successfully combat a disease, we should know the causes that contribute to it, and as much about the causes as possible. We should understand the pathological reactions of the diseased plant. Only in this way shall we be able to remove the causes or protect the plant against them or assist it to recover." If, then, we desire to find a safe remedy, we must know all that it is possible to know concerning the disease. As a link in the chain of evidence this paper is presented with the hope that it may serve to extend knowledge of the reaction of leaf tissue to fungus invasion.

HISTORIC

The relations between parasitic fungi and their host plants are of various kinds. The subject might be divided into two parts; first, the changes in the fungus when grown upon various substrata, and, second, the effects of the fungus upon its host plants. Among the latter we can easily distinguish two classes, those changes which are disturbances of the physiologic processes, and those which are changes in the morphologic structure. As we are to deal with the latter class in this paper, we shall turn our attention to the investigations on pathologic morphology which have previously been reported. The two phases which we must consider are first, the anatomic and histologic, dealing with abnormal organs and tissues, and

second, the cytologic, dealing with abnormal cell structure.

Various pathologic modifications of the floral organs have been noted. Molliard (48) described various changes in

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(48) Ann. Sci. Nat. Bot. (1895) p. 67.
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flowers caused by Peronospora, Cystopus, and other fungi as well as by insects. Wakker (84), in his most useful paper reported

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(84) Jahrbücher (1892) p. 499.
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additionally a number of abnormalities in some or all the organs of various flowers. The reproductive organs and corolla of two species^{of} Teucrium are attacked and changed in structure by the larvae of Copium (Howard, 29 and 32). Galls on the flowering

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(29) Marcellia (1906) p. 83. (32) Comptes rend. h. (1906)
p. 927.
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parts of Euphorbia cyparissias were described by Howard also, (30) and (31). The changes which Ward (86) cited as occurring

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(30) Rev. Gen. Bot. (1906) p. 67. (31) Ibid (1906) p. 241.
(86) Ann. Bot. (1888-9) p. 319.
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in the buds of Lilium candidum are less striking but none the less interesting. The effects of Cystopus candidus upon the

various organs of its host as described by Eberhardt (19) (20)

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(19) Centralb. f. Bakt. 2d Abt. (1903) p. 655.

(20) Ibid (1904) p. 235.
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are notable .

Traub (79) described the effect of Heterodera upon

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(79) Ann. Jard. Bot. etc. (1886) p. 93.
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the root structure, and other writers have also studied abnormal root structures.

Stems and branches are also subject to invasion by parasites of various kinds. A somewhat detailed description of the deformation caused by Ustilago in the stem of Zea Mays was given by Miss Knowles (35), while Wakker (84) showed that

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(35) Jour. Mycol. (1889) p. 14.
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many groups of fungi have the power of changing the appearance and structures of stems. The Exoasceae cause numerous hypertrophies and other abnormalities in the vegetative organs as shown by Smith (69). Hartman (27) described the witch-broom

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(69) Forstl. n. Zeits. (1894) p. 420. (27) Diss. Freib. (1892)

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of the white fir. Several of our common flowering plants, such

as the Hepatica and certain Euphorbias were described by Meehan
(43) as having elongated petioles and stems when attacked by

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(43) Proc. Acad. Nat. Sci. Phil. (1899) p. 108.
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rusts. Eberhardt (19) (20) gave some histologic data regarding

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(19) Centralb. f. Bakt. etc. Abt. 2. (1903) p. 655.

(20) Ibid. (1904) p. 235.
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various stem tissues in pathologic condition. Some abnormal
anatomic conditions were described by Molliard (50) .

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(50) Rev. Gen. Bot. (1898) p. 87.

The effects of disease upon the forms of leaves are
among the most noticeable of the pathologic phenomena. Woronin
(93) found various modifications of the leaf tissue caused by

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(93) Ber. Naturf. Gesells. Freib. (1867)

Exobasidium Vaccinii. Exoascus also causes very striking ab-
normalities in the leaves of various species of Prunus that
have been described by Miss Knowles (34), Atkinson (4), and

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(34) Bot. Gaz. (1887) p. 216. (4) Cornell Bull. 73 (1894).

Smith (69). Wäcker (84) described various leaf modifications

(69) Forst. n. Zeits. (1894) p. 420. (84) Jahrbücher (1892)
p. 499.

due to fungi. Some histologic changes of the needles in the
witch-broom of the white-fir were noted by Hartman (27). The

(27) Diss. Freib. (1892).

observations of Peglion (63), as set forth in his paper, showed

(63) Rivista path. veg. (1893) p. 23.

that other kinds of rusts cause changes in the structure of
leaves and stems. The anatomic changes caused by species of
Gymnosporangium were described by Wörnle (94); and Anderson (1)

(94) Forst. n. Zeits. (1894) p.68. (1) Bot. Gaz. (1897) p. 191.

described the same for Aecidium elatinum on Abies balsamea.

Plants growing normally in one range of temperature, when placed
in a colder climate are often noticeable affected. Bonnier (6)(7)

(6) Comptes rend. h. (1898) p. 307. (7) Ibid. p. 1143., (1899).

Wagner (83) and Howard (28) have given us valuable results in

(83) Sitz. d. k. Akad. Wien. (1892) 101.

(28) Comptes rend. H. (1905) p. 56.

their studies on this subject. Intumescences caused by abnormal environment have been described by Miss Dale (13) (14) (15),

(13) Proc. Camb. Phil. Soc. (1899) p. 192. (14) Phil. Trans. Roy. Soc. (1901) B. p. 163. (15) Ibid. (1906) B. p. 221.

von Schrenk (67a) and others. The effects of various chemical

(67a) Rep't Missouri Bot. Gard. (1905) p. 125.

substances upon plants have been studied. Of the work on this subject we may mention Wilfarth and Wimmer (89) (90), Crocker

(89) Jour. f. Landw. (1903) p. 129. (90) Zeits. f. Pflanz'k.
(1903) p. 82.

and Knight (12), Nemec (59) and Andrews (3). Finally we may

(12) Bot. Gaz. (1908) p. 259. (59) Jahrbücher (1903-4) p. 645.

(3) Ann. Bot. (1905) p. 521.

note that wind has been found to play an important part in the

production of abnormalities. Such observations were made by Hansen (26) and Bruck(9). The general subject of "pathological

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(26) Flora (1904) p. 32. (9) Beih. Bot. Centralb. (1906) p.67.
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plant anatomy" has been most satisfactorily reviewed by Küster (38), who has also published numerous articles upon various

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(38) Path. Pflanzenanat. (1903)
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phases of the subject, but especially concerning the anatomic features of gall-tissues (37).

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(37) Flora (1900) p. 117.

From the following review of work on pathologic cytology it will be seen that fungi, insects, poisonous substances changes of temperature, and other physical forces all tend to modify the plant cell.

Woronin (93) found that Exobasidium Vaccinii on

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(93) Ber. Naturf. Gesells. Freiburg (1867)

Vaccinium Vitis-Idaea reduces the amount of chlorophyll, and that the red colored erythrophyll takes its place in the palisade cells. When peach leaves are attacked by Exoascus defor-

mans, Miss Knowles (34) found that the epidermal cells become

(34) Bot. Gaz. (1887) p. 216.

rounded and have thickened walls, the palisade cells become nearly isodiametric, and the protoplasm is reduced in amount. Atkinson (4) found that certain of the parenchyma cells become

(4) Cornell Bull. 73 (1894)

"very much elongated and curved or sinuous in form". Tubeuf(80)

(80) Diseases of Plants (1897)

mentioned secondary cell formation in the palisade of Populus nigra in leaves attacked by Exoascus aureus. In the cells of Lilium candidum affected by a Botrytis disease, Ward (86) found

(86) Ann. Bot. (1888-9) p. 319.

that the mycelium causes a swelling, dissolving, and discoloring of the cellulose cell walls, but does not directly affect the protoplasmic parts. The same observer (87) described similar

(87) Proc. Roy. Soc. (1890) p. 393.

effects of a Botrytis disease upon the snowdrop. In Wakker's

paper (84) there are occasional references to cytologic phenome-

(84) Jahrbücher (1892) p. 499.

na. The changes noted are usually in the cell walls, the starch and calcium oxalate content, and the change in the amount of chlorophyll. Bacteria were reported by Dangeard (16) (17) as

(16)Le Botaniste (1894-5) p. 199. (17) Comptes rend. h. (1902) p. 1365.

causing the swelling of the nucleus on Euglena, the disappearance of the nucleolus, and the disorganization of the chloroplasts. The effect on the contents of cells in the process of fermentation has been studied by Matruchot and Molliard (46);

(46) Comptes rend. h. (1900) p. 1203.

and Peirce (64) has described the changes in the root tubercles

(64) Proc. Cal. Acad. (1902) p. 295.

on the Bur clover. Cystopus candidus usually causes an unusual deposition of starch and formation of chlorophyll in parts usually free from these substances, as described by Eberhardt (19) (20). Other students as Grant Smith (70), Nordhausen(61),

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(19) Centralb. f. Bak't. etc. Abt. 2 (1903) p. 655. (20) Ibid.
(1904) p. 235. (70) Bot. Gaz. (1900) p. 153. (61) Jahrbücher
(1898) p.1.

W. G. Smith (69), and Wörnle (94) have noted the effects of fun-
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(69) Forst. n. Zeits. (1894) p. 420. (94) Ibid. p. 68.
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gus-invasion upon the cellulose walls, and the distribution of
starch and of calcium oxalate. Ward (88) has found that in the
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(88) Ann. Bot. (1905) p.1.
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wheat plant the hyphae of the invading rust do not seem to af-
fect the "chlorophyll-corpuscles or the nuclei until a late
stage of growth". The leaves of the witch-broom of the white-
fir are described by Hartman (27) as having small amounts of
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(27) Diss. Freib. (1892)
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chlorophyll and starch. The Ustilagineae, according to Stroh-
meyer (75) cause various changes in the cells of the host.
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(75) Diss. Erlang. (1896)

Molliard (48) described a number of cytologic changes caused by

(48) Ann. Sci. Nat. Bot. (1895) p. 67.

insects and fungi growing on various hosts. Cystopus candidus causes the cells to assume abnormal forms and sizes, the nuclei to enlarge, and the normal chlorophyll content to change. The Peronosporas do not affect their hosts in this way. Puccinia violae on Viola silvestris causes the nuclei and the nucleoli to enlarge, and the power of division of the former to increase. The petals of Euphorbia Cyparissias when attacked by Uromyces scutellatus and U. praeminens show cells with enlarged nuclei and chlorophyll formation. The effects of various insect parasites upon the vegetable cells may be summed up in general thus: nuclei and nucleoli enlarged, chloroplasts reduced in size, often a more abundant protoplasm than normally, and variations in the calcium oxalate content. In some fungus galls Guttenberg (24) found a tendency for the nucleus to become lobed, to divide

(24) Anat. Pilzgallen (1905)

amitotically, to decrease in size, and to force the chromatin toward the periphery. The cytologic features of some gall tissues, resulting from insect invasion, has also been described by Molliard (49). The nuclei show a decided tendency toward

(49) Rev. Gen. Bot. (1897) p. 33.

amitotic division, which often results in the presence of several nuclei in a cell, with no formation of new walls. The nucleoli as well as the nuclei become greatly hypertrophied, and the former may be divided often without the subsequent division of the nucleus. At times the nucleus multiplies by a method of budding in addition to the more common means of abstriction. The nuclear membrane may finally disappear, and eventually even the nucleoli may become disintegrated. Howard (29) reported

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(29) Centralb. f. Bak't (1908) Abt. 2. p. 201.
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similar hypertrophy in the cells of the flowers of Teucrium when attacked by the larvae of Copium. Changes in root cells have been noted from time to time, especially in the studies mycorrhizas. Magnus (41) found the nucleus modified in these

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(41) Jahrbücher (1900) p. 207.
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symbiotic structures Shibata (68) notes that the nuclei in such

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(68) Jahrbücher (1902) p. 643.
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conditions become large, amoeboid, and divide amitotically. They may be strongly colored at first, but later they seem to become normal as regards division and color. Molliard (52) re-

(52) Rev. Gen. Bot. (1900) p. 157.

ported that the nematode worm lives in a tissue which has giant cells with numerous nuclei, and enlarged nucleoli. Vuillemin and Legrain (82) reported various nuclear phenomena caused by

(82) Comptes rend. h. (1894) p. 549.

the same worm in symbiotic relationship with the roots of plants cultivated in the dry Sahara region. Molliard (51) found "nu-

(51) Ibid. (1899) p. 841.

clear and protoplasmic division" in stems attacked by Phytoptus. Nawaschin (54) described strongly hypertrophied cells, and en-

(54) Flora (1890) p. 404.

larged nuclei with poor chromatin content, in tissues invaded by Plasmodiophora Brassicae. Toumey (77) noted that the nucleus

(77) Ariz. Bull. 33 (1900)

of the crown-gall cells becomes much enlarged and finally "appears as if eroded on the surface". The nucleoli are very persistent. Under abnormal conditions the root tip of Allium

Cepa shows enlarged cells and nuclei (some lacking nucleoli) and often an increased amount of chromatin. Nemec (56) also noticed nuclear fragmentation in the same root tips. The nuclei in leguminous root-tubercles are reported by Paratone (62) as

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(62) Malphigia (1901) p. 178.

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becoming amoeboid and abnormally colored. Chodat (11), however,
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(11) Congr. i. Bot. etc. (1900).

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noted no great changes. The effects of changes of temperature upon cell structure have also been studied to some extent. Prillieux (65) grew seedlings in heated soil, and found that the
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(65) Ann. Soc. Nat. Bot. (1880) p. 347.

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nuclei become numerous and variable in form. They increase by fragmentation and often possess numerous nucleoli of various shapes and sizes. These are ^{often} vacuolated. Nemec (57) found that
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(57) Sitz. d. k. Böhm. ges. Wien. (1899) #12.

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nuclei assume amoeboid forms in lowered temperatures. Schrammen (66) found changes analogous to those already mentioned in
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(66) Diss. Bonn (1902)

cells at both elevated and lowered temperatures. Matruchat and Molliard (45) (47) give very detailed descriptions of abnormal

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(45) Comptes rend. h. (1900) p. 788. (47) Rev. Gen. Bot. (1902)
p. 401.
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nuclei produced at freezing temperatures, especially noting the distribution of chromatin. Nemec (58a) produced multi-nucleated

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(58a) Sitz. Böh. Ges. d. Wiss. (1902)
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cells in the roots of Vicia faba by placing them in a one per cent copper sulphate solution. Upon returning them to normal conditions karyogamy took place and uni-nucleated cells were formed. Grant (23) has reported upon various multinucleated cells.

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(23) Trans. Bot. Soc. Edinb. (1883) p. 38.

Andrews (2) found that a nucleus, deprived of its nucleolus can

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(2) Jahrbücher (1902-3) p. 1.
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survive for a long time, but a new nucleolus is not formed.

The influence of benzene gas upon cell formation was studied by Blazek (5) who reported that simultaneous nuclear division takes

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(5) Abhandl. Böh. Akad. (1902) #17.
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place, and as many daughter nuclei are formed either with or

without subsequent cell-wall formation. Wasielewski (85) and

(85) Jahrbücher (1902-3) p. 377 and (1903-4) p. 581.

Wisselingh (91) have discussed the question of amitosis in

(91) Blätter f. Zuchern. (1903) p. 201.

various tissues. Miss Dale (13) (15) found that in certain in-

(13) Proc. Cambr. Phil. Soc. (1899) p. 192. (15) Phil. Trans.
Roy. Soc. (1906) B, p. 221.

intumescences caused by abnormal light, heat, etc., oil is formed
in place of starch, the nuclei become club-shaped and highly
refractive, and the nucleoli are often increased in number.
Amitosis was found to be almost universal, and formed nuclei
of unequal size. von Schrenk (67a) described similar intumescen-

(67a) Rep't Mo. Bot. Gard. (1905) p. 125.

ces due to chemic stimulation. Other studies upon intumescences
were made by Sorauer(71)(72) and Steiner (73). The structure

(71) Ber. d. d. Bot. Ges. (1899) p. 456. (72) Ibid (1901)
p. 115. (73) Ibid (1905) p. 105.

and the pathologic modifications of chromatophores have been studied by Nemec (55) and Küster (39). Besides these already

(55) Sitz. d. k. Böhm. Ges. Wiss. (1897) #23. (39) Zeits. f. allg. Phy. (1904) p. 221.

enumerated it would be well to note the following as articles dealing with several phases of the subject, and containing valuable lists of reference. Zimmerman (96) (97), Ward (87),

(96) Morph. u. Phys. Pflanzenz. (1887) (97) Morp. u. Phys. p. Zellk. (1896). (87) Proc. Roy. Soc. (1890) p. 393.

Unger (81), Fairchild (21), and Nemec (60). Some nuclear phenomena

(81) Sitz. d.k. Akad. (1864) p. 132. (21) Ber.d. d. Bot. Ges. (1894) p. 331. (60) Ibid. (1905) p. 113.

mena have been described also by Miehle (44), Kohl (36), and

(44) Flora (1901) p. 105. (36) Bot. Centb. (1897) p. 168.

Zacharias (95).

(95) Flora (1895) p. 217.

Summing up these effects of parasitic invasion and abnormal physiologic influence upon the histologic and cytologic elements of plants, we find that the various kinds of tissues, collenchyma, parenchyma, schlerenchyma, and cork may be abnormally developed or repressed; cell walls may be simply perforated, or much thickened and more or less changed in constitution; secondary cell formation may arise; nuclei and nucleoli may be increased or reduced in number and size, and variously deformed; chromatin may likewise be increased or decreased; the cell sap may acquire a new color; the starch and calcium oxalate content may change; and the chromatophores changed in appearance and efficiency.

METHODS

The ordinary methods of preserving the material were used. The medium solution of chrom-acetic acid was found to be the most useful killing and fixing fluid experimented with. Picric alcohol was less satisfactory because of its poorer fixing power, and because stains of several kinds refuse to affect the tissue when preserved in this solution. For the same reasons picro-nigrosin was not very successful. An abundance of material was usually kept in the dry condition as herbarium specimens, and some was preserved as well in four per cent formalin. Paraffin, melting at about fifty-two degrees centigrade, was used for most of the work, though the harder grade

melting at sixty degrees was employed for some of the tough, resistant leaf tissues.

The orseillin-anilin-blue method of staining as outlined in Strassburger's Practicum (74a) was used for all of the

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(74a) Das Botanische Practicum (1902) p. 685.
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preliminary work. This combination serves to differentiate the fungus in the host tissue, and also to make it easy to distinguish the cell contents. The latter stains rather darkly with orseillin, and the host cell walls lightly with the anilin blue. The fungus-walls stain much more deeply with the anilin blue. Later in the work, when studying the nucleus, Haidenhain's haematoxylin was used, about as outlined in Methods in Plant Histology by Chamberlain (10). The differentiation thus ob-

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(10) (1905) 2d ed. p. 33.
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tained was very satisfactory, since the nucleus held the stain more tenaciously than did the cell walls. Fuchsin also was used to some extent.

About fifty different specimens were preserved, sectioned, and examined. Many of these failed to be of value, either because of the great destruction of the host tissue by the fungus, or because of the absence of distinctive or recognizable cytologic changes. The drawings were all made with a

Bauch and Lomb camera lucida; and a twelfth inch, achromatic, oil immersion objective of the same make was used for all high magnifications in all camera drawings. The drawings are, with one or two exceptions, of the same magnification, and hence can be compared directly with one another. The attempt was made to get satisfactory material which would illustrate as great a diversity of host plants, as well as of fungi, as possible. In the following pages, therefore, there will be representatives of both Monocotyledons and Dicotyledons, and of the latter from several diverse families. The Uredineae and the Fungi Imperfecti are the chief groups of fungi represented.

OBSERVATIONS

1. *Gaylussacia baccata* (Wang.) C. Koch, parasitised by

The normal leaf tissue is composed of the following: (1) a single layer of nearly isodiametric cells in the upper epidermis; (2) a single layer of palisade cells; (3) a rather loose spongy parenchyma with comparatively large intercellular spaces; and (4) a lower epidermis of cells usually somewhat smaller than those of the upper epidermis. The plant studied was collected in early summer, and hence the leaves were fully formed, but still in a vigorous condition. The location of the plant was at the edge of a wooded area, but in the open, so that the leaves received an abundance of light. The leaf cells have a thin peripheral lining of protoplasm in which the chloro-

plasts and the nuclei are imbedded. The cuticle is nearly colorless, and much thicker over the upper than over the lower epidermal cells.

The parasitised leaf shows a number of changes. Just before the palisade cells, and after the sponge cells, begin to collapse, they are filled with a uniformly brown-stained material. Previous to this they are filled with a granular mass which is stained yellow-brown. In both of these stages of degeneration there are neither chloroplasts nor nuclei to be seen. At the same time the upper epidermal cells become considerable elongated, and the cuticle is light yellow to brown. In the last phase of degeneration the epidermal cells become completely collapsed, the palisade cells are much shrunken, and the sponge cells have practically disappeared, while the cell walls are uniformly brown, and the cells empty.

2. *Viola cucullata* Ait. (?), parasitised by *Puccinia Violae* (Schum.) DC.

The normal leaf tissue of this plant is rather poorly differentiated. The epidermal cells are very irregular in shape and size, and the cuticle is thin. The mesophyll is composed of a loose mesh of rounded cells stretching from one epidermis to the other. The tissue is evidently very easily ruptured and is seldom complete except at the veins and in connection with the fungous spore-beds. The plants examined were

growing in a well shaded and damp location, and were collected in early summer.

In these parasitised regions the cells are closely compacted, and more or less bound together by the invading mycelium which fills the intercellular spaces. Here also the haematoxylin stains much more intensely than in the normal tissue. There seems to be some hyperplasy of the mesophyll. The epidermis is ruptured by the spore bed, but the influence of the fungus does not extend far beyond this radius. The nuclei, which are not prominent in the normal cells, become somewhat enlarged, and increase in number in the cells. There are numerous instances where the number is increased to two, while some cells were noticed that contain three nuclei. The nuclei are also more or less deformed, varying from nearly circular in cross-section to oval, oblong, or slightly pear-shaped. The chloroplasts seem to be little affected, at least in shape and size, by the presence of the parasite.

3. *Psedera tricuspidata* (Sieb. and Zucc.) Rehder, parasitised by *Phyllosticta labruscae* Thum.

The normal leaf tissue is similar to that of the Gaylussacia described above, and the pathologic changes are very much alike in the two plants. The browning and collapse of the epidermal, palisade, and sponge cells are common to both. The early disappearance of nuclei and chloroplasts is also similar in the two. There is in this case a granular protoplasm

in the cells next to the dead area, while the homogeneous brown mass is not formed. The sponge tissue is more completely disorganized than the palisade. This plant, collected in early July was growing upon a wall exposed to the morning sun.

4. *Smilax glauca* Walt., parasitised by

The leaf parenchyma is not differentiated into palisade and sponge tissues. The diseased area is badly shrunk and broken down. The fungus-perithecia are scattered irregularly over this dead area. Because of the thorough killing of the host tissue, no special cytologic changes could be noted.

5. *Potentilla canadensis* L., parasitised by

There is a double parasitism represented here. Darluca filum was found growing abundantly upon the spore-beds of the rust, and at times apparently directly upon the leaf tissue of Potentilla. This latter condition, however, may have been due to the rust mycelium in the tissues which had not yet produced a noticeable spore bed.

The normal structure of this Potentilla leaf is somewhat more complex than that of the Viola described previously. The palisade cells have a more oblong longitudinal section than the sponge cells and are more closely packed. The plants collected were growing in a place which was shaded all of the afternoon and part of the morning. The collection was made

about the middle of July.

When the leaf is attacked by the rust, the epidermis is broken, the palisade is poorly developed, and more or less replaced by rounded cells common to the sponge and the diseased palisade tissues. In the early stages of the disease the lower epidermis separates from the mesophyll. There is some hyperplasy of the sponge tissue. The cells, which remain in the tissue directly under the spore beds, are widely scattered and separated by the mycelium of the rust. When the rust is parasitised by Darluca the palisade tissue is less abnormal and disorganized. The chlorophyll seems to have largely disappeared from the cells which are within the influence of the rust. A similar effect upon the nuclei is usually seen. An increase in the number of nuclei in individual cells was noticed, however in tissue just below a perithecium of Darluca, which was found imbedded directly in the tissue of the Potentilla leaf.

6. *Panicum latifolium* L., parasitised by

The normal leaf tissue is that of the ordinary grasses. The epidermal cells on both sides of the leaf are very large as compared with the simple mesophyll cells which occupy the space between the two layers of epidermis. In the healthy chlorophyllose cells there is only a ^hthin peripheral lining of protoplasm in which the nuclei and chloroplasts are distributed.

Many of the cells of the diseased area are filled with a homogeneous substance which stains blue, so that at a

glance the location of the diseased tissue can easily be discovered. The protoplasm, which is somewhat more abundant and more evenly distributed in the diseased cells than in the normal, is very finely granulated. Many of the diseased cells show two nuclei. All of the nuclei in the vicinity stain deeper or retain the stain more tenaciously than in the healthy tissue, and are relatively larger than in the normal cells. The chlorophyll has largely disappeared from the cells close to the point of invasion, but farther away the chloroplasts are merely reduced in size.

7. *Pyrus malus* L., parasitised by *Gymnosporangium* sp.

The structure of this leaf is somewhat more complex than of any of those previously described. The upper and lower epidermal cells are in single layers, and are partly isodiametric and partly oblong in shape. The palisade cells, which are in two layers, have their nuclei symmetrically placed in the peripheral protoplasm close to the middle of the lateral walls. The chloroplasts are also arranged along the same walls. The cells of the upper palisade layer are about a third longer than those of the second layer, and about the same width as those cells. This palisade occupies half the thickness of the leaf. The sponge cells^{are} loosely connected and have large air chambers scattered among them. The tree, from which the diseased leaves were taken, was growing in a thicket, and about fifty feet from a Juniperus tree.

The portion of the leaf which is parasitised is about twice as thick as the normal tissue. This thickening is due to two factors, the hypertrophy of the sponge tissue, and the presence of masses of mycelium. The palisade cells are least affected. The cells in the upper layer are shortened until they are about the length of the cells in the second layer. The space thus left between the upper epidermis and the palisade cells is occupied by mycelium from which the pycnia are developed. The upper epidermis is puffed up and ruptured, the cells are nearly collapsed, the walls are changed to a brown color, and the cuticle is mostly destroyed. The parenchyma cell walls seem to remain about normal. The sponge cells are enlarged to twice or thrice their normal diameters, and the spaces between are filled with the heavily stained mycelium. The nuclei of the sponge cells are the first to show the effects of the presence of the fungus by becoming rather larger than they are normally. They are not, however, otherwise materially changed. Many cells are partially filled with a yellow, granular deposit.

8. *Smilacina racemosa* (L.) Desf., parasitised by *Phyllosticta cruenta* (Fr.) Kicks.

The leaf of *Smilacina* is rather simple in structure. The upper epidermis has relatively large oblong cells interspersed, at intervals, with short cubical cells. The lower epidermis has smaller, and usually more regular, cells. Between these two layers is a rather loose parenchyma with large

air spaces, and with the larger number of cells close to the upper epidermis. The plants collected were growing at the side of a road through the woods, where the light was rather weak and there was abundant moisture.

In the diseased area the cuticle and the epidermal cells are affected to a greater distance from the center of infection than the sponge cells. They are early turned brown, and the epidermis is shrunken. The sponge tissue is badly disorganized, but chloroplasts and nuclei are present. The latter attain a larger size, and have a light brown color whereas when normal they are easily stained with haematoxylin. They often have two nucleoli and a granular plasm. Later in the degeneration of the nucleus the nucleoli disappear and the nucleolus stains deeper. The chloroplasts may later disappear and afterward the other constituents of the cell.

9. *Castanea dentata* (Marsh.) Borkh., parasitised by *Cryptosporium epiphyllum* C. and E.

The normal leaf is covered by an epidermis with cells rather larger than those of the sponge tissue. The palisade tissue, which is composed of very long narrow cells, sometimes with a row of short cells below, occupies about half the total thickness of the leaf. The sponge is very loose, and has large air chambers. The cells of the lower epidermis are smaller than those of the upper.

As examined in prepared material the diseased area is very sharply separated from the healthy part of the leaf. There are practically no cells that show transition phases between the normal and the diseased conditions. The epidermal cells over the parasitised portion are flattened, and often filled with granular deposits which have also been noticed in other diseased plants. The palisade and sponge cells are much shrunken and the entire contents was killed apparently before the specimen was collected. The entire diseased area is yellow-brown, while the normal tissue stains easily with anilin blue. No cytologic changes are to be seen except the deposit of the yellow-brown material throughout many of the cells, and the occasional enlargement of the nucleus. In some cases the palisade tissue has thus been affected, while the sponge cells are less noticeably changed.

10. *Xanthium canadense* Mill. (?), parasitised by *Puccinia Xanthii* Schu.

The normal leaf tissue is very loosely formed between the upper and lower epidermal layers. The palisade is scattered, and the sponge is permeated by very large air chambers. Transitional phases between the normal and the diseased conditions of the host cells were not found.

This tissue is more profoundly altered than any other under discussion. It is in many places almost completely replaced by the fungus-mycelium. The cells which remain have no

protoplasm and are filled with oil globules. On both the upper and the lower leaf surfaces the mycelium is abundant, and the telial spores are very numerous. Within the mixture of parenchyma cells and mycelium, which replaces the normal tissue, there are cyst-like bodies which are composed of masses of mycelium. These objects are hollow spheres and from the inner surface arise telial spores exactly similar to those borne in the normal way upon the exterior of the leaf. Part of the mycelium near the exterior stained brown while that within the host tissue stained blue with the anilin blue.

DISCUSSION AND CONCLUSIONS

The changes which are caused in leaf tissue by parasitic fungi are similar to those which have previously been reported as occurring in other parts of phanerogamic plants, and caused by insect invasion, changes of temperature, and parasitic fungi. A comparison of the observations reported in the latter part of this paper with those of other workers reviewed in the earlier part, will show that the enlarging, changing of form, and dividing of the nucleus, the changing of the composition of the cell walls, the reduction in the amount of chlorophyll, and other changes in the normal content of the leaf cells, are all duplicated in other organs affected by destructive agents.

These changes are usually only variations of natural processes, and are not phenomena that are known only in patho-

logic tissues, for it is to be noted that these changes in the appearance of the nuclei are not unknown in normal vegetable cells. Johow (33) describes amitosis as occurring in the older

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(33) Bot. Zeit. (1881)

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cells of Chara foetida. The presence of two or more nuclei in a cell has been noted by Treub (78) in bast cells of various

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(78) Archiv. Neerl. d. Sci. exact etc. (1880), 15, p. 39;
Comptes rend. (1879) p. 494.

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plants; while a process of division is reported by v. Bretfeld (8) and Massart (42) as so common in wound tissues that they

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(8) Jahrbücher (1880), 12, p. 133. (42) mem. etc. Acad. Belg.
(1898) p.3.

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believed that nearly all such tissue is formed by the "amitotic" process as they called it. More detailed work is necessary to show whether the amitotic process of Johow and the processes of nuclear division in wound and diseased tissues are really analogous, since the former process seems to be for the purpose of increasing the nuclei in connection with the metabolism of mature cells, and the latter processes often lead to an increase in the number of cells and are found in cells apparently stimulated to a kind of rejuvenescence. Schürhoff (67b), however,

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(67b) Beihefte z. Bot. Centralb. (1906), 19, p. 359.
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has shown that this idea is far from correct, since there are many cases of mitosis in wound tissue, and no true amitosis is certainly known in these tissues. A process that appears to be true amitosis has been reported by Shibata (68) in mycorrhizal

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(68) Jahrbücher (1902), p. 643.
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cells and by Tischler (76) in Heterodera galls on Circaea.

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(76) Ber. d. d. Bot. Gesel. (1901), p. 35.

A rather detailed discussion of this question is given by Miss Dale (15); while Küster (40) and Strasburger (74b) review the

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(15) Phil. Trans. Roy. Soc. (1906) B, 198.

(40) Ergb. d. allg. Path. etc. (1906) 11. (74b) Prog. rei Bot.
(1906)

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whole subject of the direct and indirect methods of nuclear division.

No nuclei were noted in actual process of division, but in a few instances there is some evidence of abnormal division. In Potentilla (fig. 4) such is the case. The nucleus is somewhat elongated, and at one end is stretched out into a

conical point. A comparison of figure 4 with Häcker's (25)

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(25) Anat. Anz. (1900), p. 9.
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figures 9, 10, 14, and 16, will show the close resemblance between the nuclei supposed to have divided recently (fig. 4), and the actual process as reported by Häcker. A case which is less clearly related is seen in figure 1, where the nucleus is pear shaped. Whether or not these are cases of true amitosis or of pseudoamitosis could not be determined, as only the end products were seen.

The composition of the cell walls of the host may be changed. Two evidences of this are forthcoming. In Panicum especially, it was noted that the walls of the parasitised cells are more deeply stained than those of the ordinary cells. Since the walls are not noticeably thickened the only remaining explanation is that some change in the chemical or physical composition of the walls has taken place, in such a way that they have a greater affinity for the stain, anilin blue. In most of the diseased tissues the walls become brown. This color is probably due to the formation of tannins. There is always more or less of these substances in the walls, and when the cells begin to die it is known that this browning often takes place through the work of the tannins. In several cases also, granular deposits were found in various cells in the diseased regions only, of Castanea, Pyrus, etc., similar to those described by

Zimmerman [(98) § 207] . Just what would cause this precipita-

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(98) Bot. Microtechnique (1896)
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tion is not clear.

It was not always possible to determine which constituents of the host cell first showed the effect of fungous invasion. It is evident, however, that there is no general rule to be laid down. In Smilacina, for example, the chloroplasts seem to disappear before any of the other cell contents, while in Pyrus the nuclei of the sponge cells become enlarged before there are any other signs of change. It has already been pointed out that in some cases the cuticle and epidermis are affected first as the fungus spreads from the center of infection, while in other cases no such result was observed.

The effects of the rusts upon the leaf tissue~~s~~ are similar to those of gall producing insects. The nuclei are enlarged the protoplasm is often increased, and there is considerable hypertrophy. In other words the rusts seem to stimulate the tissue rather than to retard its growth. The witch~~x~~-brooms are evidences of such an influence, and Molliard (49) describes

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(49) Rev. Gen. Bot. (1897) p. 33.
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such effects caused by insects in several hosts.

The effects of the fungous invasion upon the proto-

plast are various. At times the nuclei may entirely or almost disappear from the diseased area, leaving the cells, thus deprived of the nucleus, in a dead condition. This was noted in Potentilla and Gaylussacia. In other cases there is an unusual activity in the nuclear divisions, resulting in several nuclei in one cell. Viola and Panicum have already been cited as examples of this. The fact has already been given that the nuclei may also become larger than normal. The chromatin content of the diseased nuclei seems at times to become greater also. Such a condition is seen in Panicum in which the nuclei of the diseased cells stain more intensely with haematoxylin than those of the normal cells. This may not be due to an actual increase in the chromatin, but either to a relative increase in the nucleic acid, or to a physical rearrangement of the chromatin. The chloroplasts may be reduced in size and finally disappear as in Potentilla, or they may, as in Viola, persist until the final disintegration of the cell. The differences in the reactions of the cytoplasm and of the cell walls have already been cited in other connections.

With the attacks of parasitic fungi on leaves the effects are varied, depending upon the species of the host and of fungus. The virulence of the parasite and the degree of resistance of the host are the chief factors involved. If the leaf, while in an actively growing condition, is attacked by the fungus, the changes in the host are often profound, if the fungus is able to maintain itself against the protective meas-

ures put in operation by the host. The cytologic changes already described are likely to occur. The leaf curl of peach caused by Exoascus deformans is an example of this type of change. Miss Knowles (34) has described the leaf structure in

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(34) Bot. Gaz. (1887) p. 216.
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this disease and has found that the tissue is greatly altered by the presence of the fungus. The leaves are attacked in the bud or very soon after their emergence (Duggar 18). Cytologic

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(18) Exp. Sta. Cornell Bull. 164 (1899)
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changes may also occur when the fungus acts slowly for any reason. If the fungus is a weak parasite or if the host is not the one best suited to the fungus, the host will have time to react to the fungus, and notable changes may be expected, both in the cell and in the tissue as a whole. That there is a difference in the speed with which various parasites work is seen from the fact that some diseased tissues show cells in various degrees of degeneration or death, while in others there are no intergrading conditions between the dead, brown cells of the diseased area and the normal cells of the healthy tissue. The Gaylussacia described above shows relatively slow action of the parasite, as is proved by the two following conditions. First, the cells react by showing a granular protoplasm, then a uni-

form mass of broken down protoplasm, which is stained brown, and finally nearly empty cell walls. It is improbable that this gradual degeneration is merely a process that would normally take place in cells which are breaking down, because often, as in Castanea none of these intergrading forms is found. Second, it is to be noted that in Gaylussacia, and other hosts reacting similarly, the cuticle and the epidermal cells are often affected before the mesophyll, as the fungus spreads from the centre of infection. This tends also to prove that the fungus acts progressively and slowly enough to be observed in the successive steps. Psedera, Viola, and Panicum act somewhat similarly in that they show changes in the size and number of nuclei, etc., as cytologic changes induced by the slow action of the respective parasitic fungi.

In some of the diseases described, in which the tissue is killed and badly disorganized, few, if any, cytologic changes are to be noticed. The reason for this seems to be that the virulence of the fungus is relatively so great that the cells of the host are killed without having time to react to any stimulus. In such cases, as in Castanea, all tissues seem equally affected, and there are no transition cells from the healthy to the dead portions. Another factor also which may operate is that the host tissue is old, and has not the power of reacting rapidly. This is in contrast with the young, highly resistant tissues, which, if parasitised, are able to react rapidly, and so present abnormal nuclear and other cyto-

logic phenomena. Smilax also is an example of a diseased tissue which shows no cytologic changes.

A question constantly before the student of pathology is whether there is any way of judging the degree of susceptibility of a plant to disease. First of all it must be remembered that a plant may be easily attacked and injured by one disease-producing organism, and be quite immune to the attacks of another. Leaving this phase of the question, however, we ask "Is the amount of hypertrophy a true indication of the degree of parasitism?" If we imply in the word "parasitism" some influence derogatory to the welfare of the plant, we are almost forced to answer the question in the negative, for in cases of symbiosis there is often great hypertrophy.

It is difficult at present to draw a sharp line between parasitism and symbiosis, since similar effects upon the host are noted in both. Thus in some of the most noted instance of symbiosis, the mycorrhizas, there is often considerable hypertrophy. Moreover, many kinds of galls do not seem to injure the hosts beyond the local tissue, and here again there is great hypertrophy. Hence, taken alone, an excessive enlarging of a portion of a plant is not sufficient evidence of the degree of parasitism. But taken in conjunction with the cytologic changes induced in the host, hypertrophy becomes a valuable diagnostic feature. It must not be forgotten, however, that even in such cases the parasitic nature of the organism is not proved, for cytologic changes in mycorrhizas have been

reported as noted heretofore. Evidence has previously been given in regard to the diagnostic value of the cytologic changes in such tissues as the leaves of Pyrus and Xanthium. Here the hypertrophy is coincident with the changes in the constitution of the cell, and it indicates a rather strong parasitism. On the other hand, as in Psedera and Gaylussacia the virulence is so great that the cytologic changes are simply the fleeting features of a rapid degeneration, and of course no hypertrophy could take place. Here again the condition indicates a strong parasitism. v. Tubeuf (80) points out that the degree of sus-

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(80) Diseases of Plants (1897) trans. by W. G. Smith. p. 48.
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ceptibility of the host, or in other words, the degree or strength of parasitism is indicated by the amount and kind of deformation, as has just been indicated. He draws his illustration from the Uredineae. He says, " If the host suits the fungus only in a limited degree, then no hypertrophy will result, and the latter will attain only to the formation of spermatogonia. Let the host, however, be the one best suited to the fungus, then hypertrophy will result and aecidia be developed." He gives as evidence a series of experiments upon Gymnosporangium in which the fungus developed to different degrees varying with the host used. Fenstling (22a) in discussing the ef-

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(22a) Diss. Freiburg (1892)
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fect of rusts upon their hosts comes to the same conclusion regarding the relation of the degree of change to the time of the fungus attack.

In the leaf inhabiting fungi so far as studied, the mode of attack seems to be through the aid of some substance injurious or stimulative to the host cells. Two lines of evidence are at hand. The protoplasm of cells outside of the tissue directly in contact with the fungus often becomes killed, and the cell walls become brown. It is difficult to see how such a condition could exist if there is no toxic substance produced. In the second place, most of the cells of the host tissue, examined by the writer, contained no trace of the fungus, yet, as already shown, the nuclei are often enlarged or become numerous, and the chloroplasts also are reduced in size. Here again, there must be a substance which is diffusible through the cell-walls, which is stimulative to the nucleus or poisonous to the chloroplasts. No indications were to be found as to the origin of such a substance. It is possible that the host cells may have produced it as a defensive measure, and that in turn certain of the cells were killed by this toxic substance. On the other hand it is possible that the fungus may produce such a poisonous substance which directly affects the host cells, as Ward (86) claims for the *Botrytis* fungus that causes

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(86)Ann. Bot. (1888-9) p. 319.
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the Lily disease. Woronin (93b) attributes in an inferential

(93b) Mem. Acad. Sci. St. Pet. (1888)

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way the effect of Sclerotinia Vaccinii upon the cowberry to the same process. Tubeuf (80) quotes from him thus: "Here a pecu-

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(80) Diseases of Plants (1897) p. 259.

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liar phenomenon is exhibited, the fungus exerts its injurious effects on the surrounding tissues of the host-plant, then, having killed these, it utilizes them as food material." Thus the tissues are killed first, apparently even beyond the immediate vicinity of the fungus, and are later used for food.

That the parasitic fungi upon leaves produce this toxic substance is more easily believed than that the host produces it, and is itself killed by the protective measure. The nature of the poisonous substance, whether a chemical, ^{or an} organic poison or an enzym, could not be determined in the material at hand.

SUMMARY

In the review of previous work it was found that many changes have been noticed in the organs and tissues of flowering plants. The cytologic changes, however, were especially emphasized. Very little work has previously been reported

upon the effect of fungi on the cell contents of leaves, and the writer has shown that in such cells the nuclear and protoplasmic changes, which other workers have noted in cells of other plant organs attacked by parasites or under the influence of other destructive agents, also occur in leaf tissues when attacked by the parasitic fungi examined.

I wish here to thank Dr. T. J. Burrill, under whom these investigations were carried on, for the privileges of the department extended to me, and Dr. H. A. Gleason and Dr. Charles F. Hottes of the Department of Botany, for their kindly criticism of portions of the manuscript of this article.

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302

Ernest Shaw Reynolds was born in Glendale, Montana, December 7th 1884. Both of his parents are graduates of the University of Illinois in the class of 1874. The family moved to Providence, Rhode Island in the summer of 1891, where their son Ernest entered school the following September. In June 1898 he completed the graded school course; spent the next year in the Preparatory Department of the High School instead of the final year (the ninth) of the grades and in June 1903 he received an English Department Diploma from the Hope Street High School. The following fall he entered Brown University, and while there was an assistant for three years in the Botany Department. Having practically completed the four years work at the end of his Junior year he took a year of graduate work, and in June, 1907, was awarded the Ph. B. and the A. M. degrees. Botany and chemistry were his special subjects for advanced work. During the summer following graduation he was an assistant at the Gray Herbarium of Harvard University, and in the fall went, as Fellow in Botany, to the University of Illinois.

Mr. Reynolds was elected a member of the New England Botanical Club of Boston during the winter of 1906, and the Illinois chapter of Sigma Xi during the fall of 1908. He is a charter member also of the Illinois Academy of Science and of the Illinois chapter of Gamma Alpha Graduate Scientific Fraternity. A paper upon the "Flora of the Great Swamp of Rhode Island" was published by him in the July number of Rhodora 1907. A note on "*Scirpus hudsonianus* in Rhode Island"

appeared in the January issue of the same magazine in 1908, and a paper, entitled "Plant Pathology in its Relations to Other Sciences" was published in Science, June 19, 1908.

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