THESIS

on

STUDIES OF YELLOW RUST OF RUBUS

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by

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>History and Distribution of the Disease</td>
<td>1</td>
</tr>
<tr>
<td>Purpose of the Investigation</td>
<td>3</td>
</tr>
<tr>
<td>CAUSAL ORGANISM</td>
<td>3</td>
</tr>
<tr>
<td>Classification</td>
<td>3</td>
</tr>
<tr>
<td>Life History and Morphology</td>
<td>7</td>
</tr>
<tr>
<td>Methods</td>
<td>7</td>
</tr>
<tr>
<td>Pycnia</td>
<td>9</td>
</tr>
<tr>
<td>Field Observations</td>
<td>9</td>
</tr>
<tr>
<td>Greenhouse Experiments</td>
<td>10</td>
</tr>
<tr>
<td>Histological Studies</td>
<td>10</td>
</tr>
<tr>
<td>Aecia</td>
<td>13</td>
</tr>
<tr>
<td>Field Observations</td>
<td>13</td>
</tr>
<tr>
<td>Greenhouse Experiments</td>
<td>16</td>
</tr>
<tr>
<td>Histological Studies</td>
<td>19</td>
</tr>
<tr>
<td>Uredinia</td>
<td>22</td>
</tr>
<tr>
<td>Field Observations</td>
<td>22</td>
</tr>
<tr>
<td>Greenhouse Experiments</td>
<td>26</td>
</tr>
<tr>
<td>Histological Studies</td>
<td>27</td>
</tr>
<tr>
<td>Telia</td>
<td>29</td>
</tr>
<tr>
<td>Field Observations</td>
<td>29</td>
</tr>
<tr>
<td>Histological Studies</td>
<td>31</td>
</tr>
<tr>
<td>HOSTS</td>
<td></td>
</tr>
<tr>
<td>Varietal Susceptibility</td>
<td>35</td>
</tr>
</tbody>
</table>
STUDIES OF YELLOW RUST OF RUBUS

1.

INTRODUCTION

The yellow rust under consideration here is a disease which occurs on certain species of the genus Rubus. The common name, "yellow rust" is derived from the dusty, yellow spore stages which are found on the leaves and canes during the spring, summer, and fall seasons. The disease is found particularly prevalent in the Pacific Northwest, where it has assumed economic importance as a detrimental factor to the berry-growing industry.

HISTORY AND DISTRIBUTION OF THE DISEASE

Zeller (16,17) has reported development of the disease to damaging proportions on the Cuthbert red raspberry in this region. Leaf infections, and cane lesions are the two chief sources of trouble. Leaf infections sometimes become numerous enough to produce partial defoliation and devitalization of the whole plant may result.

Stem infections cause the greatest economic losses. Zeller (17) reports that the greatest damage occurs during the second or fruiting year of the canes. Lesions produced on the canes during their growth become deep and cankerous by the second year and may hinder the flow of sap, produce a brittleness of the canes, and cause a drying of the berries before they reach maturity. These cane lesions offer
2.

a subsequent source of secondary infection by other fungi. Cane blight of raspberry (*Leptosphaeria coniothyrium*) has been found to enter through the rust lesions on the canes and to extend its infection from there. (16)

Yellow rust is known to occur in Europe and in all northern parts of the United States and southern Canada. Its geographical range in America extends from Newfoundland and Massachusetts to Colorado and northern California, and northward into the Canadian provinces. (16)

It has been reported as occurring autoeciously on *Rubus leucodermis* Douglas, *Rubus occidentalis* Linn., *Rubus spectabilis* Pursh, and *Rubus strigosus* Michx., and that the most severe attacks occur on *Rubus strigosus* Michx. (red raspberry) and *Rubus spectabilis* Pursh (Salmon-berry). *Rubus strigosus* has been reported as having the widest distribution of the species of *Rubus* and its occurrence on that host has been found in Canada from Newfoundland and Nova Scotia to Ontario and into British Columbia. In the United States it is distributed from Maine and Massachusetts to Montana and Colorado, and in Oregon and Washington. (16)

The disease is reported as general in northern Europe and extends south into Italy. It is also reported in the British Isles. (13)

Aside from the work of Zeller in 1927, (16) a study of the literature pertaining to the yellow rust disease reveals that no investigations of the life history of the organism have been undertaken. Zeller describes the external morph-
ology and the spore stages to some extent. His studies were principally concerned with field observations on the occurrence of each stage under Oregon conditions. The brief mention of this rust in United States Department of Agriculture Farmer's Bulletin No. 1488. (11), is based on Zeller description of the disease. It states that Cuthbert and Antwerp red raspberries seem most susceptible.

PURPOSE OF THIS INVESTIGATION

The present investigation was undertaken with hope that a more comprehensive understanding of the yellow rust organism and its relation to the host might result. Certain phases in the life of the organism needed further study, and special attention was given to (1) what is known of the classification of the organism causing yellow rust, (2) the relation of host and parasite as revealed by an histological study, (3) nuclear conditions and relations between the different stages of the rust, (4) conditions bearing on infection, and (5) susceptibility of different species and varieties of Rubus.

CAUSAL ORGANISM

CLASSIFICATION

The fungus responsible for the Yellow Rust of Rubus belongs to the genus Phragmidium. The species of this genus
are all autoecious, and include pycnia, aecia, uredinia, and telia in their life cycle. The pycnia are usually subcuticular, while the aecia and uredinia are characteristically subepidermal in the leaf tissue. The aecia are of the caeoma type, in that they do not produce a peridium. Paraphyses are present however. The genus is particularly characterized by the teliospores which have two or more parallel septa and are pediculate. (14)

*Phragmidium imitans* Arthur is the name which has for some time been applied to this rust fungus in the United States and Canada. It was originally described in America under the name *Phragmidium gracile* Arthur, but since this was untenable, it was changed to *Phragmidium imitans* by Arthur in North American Flora. (1)

During the preliminary work on this organism it was noted that a very similar species (*Phragmidium Rubi-Idaei* (DC.) Karst.) is prevalent in Europe. The question arose as to whether *Phragmidium imitans* Arthur is the same as *Phragmidium Rubi-Idaei* (DC.) Karst.

Grove briefly mentions *Phragmidium imitans* Arthur as very similar to the European species. He describes it as having similarly formed caeomata and as being found on allied species of Rubus. (12). Zeller (1927) (16) has also notes its similarity to *Phragmidium Rubi-Idaei* (DC.) Karst.

In a recent paper on the classification of 19 species of *Phragmidium* occurring in North America, Cummins (10),
one of Arthur's students, has two keys. One key takes into consideration the differences in teliospore characters. The second key includes the same 19 species under the same host tribes, but uses as its basis the characteristics of the aeciospores. Three host-type groups are provided for, namely, Potentilleae, Rubeae, and Roseae. The two divisions Earlea and Euphragmidium of Arthur are used in classifying teliospore characters in the first key. The first division has listed under its heading those forms which have firm, non-hygroscopic teliospore pedicels. Teliospore characteristics are used as a bases for separating the species under each of the three host tribes.

In the second key classification is determined according to the surface of the aeciospores.

It is significant to note that Cummins does not include Phragmidium imitans in this monographic key to North American species of Phragmidium, but does include Phragmidium Rubi-Idaei, the European species. This would indicate that Arthur and Cummins both consider them synonymous. The description of Phragmidium imitans given by Arthur in "North American Flora" and that of Phragmidium Rubi-Idaei given by Grove in "British Rust Fungi" for the European species were compared by the writer. Thanks to the courtesy of Dr. E. J. Butler, dried specimens of urediniospores and teliospores of Phragmidium Rubi-Idaei were secured through the British Imperial Mycological Institute. These had been collected in August,
1931, from wild raspberry plants (Rubus idaeus) in England. The only aeciospores of **Phragmidium Rubi-Idaei** obtainable at the time were from No. 130, Briosi and Cavara Exsiccati (5), in the Herbarium of the Botany Department of Oregon State College. These spore stages were used as a check against Oregon material of the fungus and the type of **Phragmidium imitans** Arthur from Decorah, Iowa, from Nos. 518 and 1124, North American Urediniales. (3)

In view of the similarities found in the American and European specimens studied the writer believes that **Phragmidium imitans** Arthur and **Phragmidium Rubi-Idaei** (DC.) Karst. are the same organism, and that the older European name should be used.

**Phragmidium Rubi-Idaei** was originally described by De Condolle under the name *Puccinia Rubi-Idaei* DC. Karsten later transferred the species to Phragmidium.

Saccardo (13) and Grove (12) have given most of the other synonyms which have been applied to **Phragmidium Rubi-Idaei** (DC.) Karst. Saccardo gives the original description as amended by Karsten. In this the aeciospores are described as 20 - 28u. in diameter, and the urediniospores as elliptical to ovoid and 16 - 22u. in diameter. Teliospores are described as 5 - 10 septate (averaging 6 - 8) and from 90 - 160u. long and 17 - 35u wide. *Rubus Idaeus*, *Rubus odoratus*, and *Rubus strigosus* are the three susceptible hosts given.
Cooke (1875) (7) under the name *Phragmidium gracile* Cooke merely gives illustrations of the teliospores and aeciospores. Grove (1913) (12) gives a more complete description of the spore stages.

**LIFE HISTORY AND MORPHOLOGY**

The life history and morphology of *Phragmidium Rubi-Idaei* were considered through the structure, nuclear condition, and function of the four sporulating stages, namely, the pycnia, aecia, uredinia, and telia.

**Methods.** - The Cuthbert variety of red raspberry was used in all the experiments performed. Each stage of the rust was studied under field conditions, under greenhouse conditions, and histologically.

During the year 1931, field observations were made in the vicinity of the Oregon Experiment Station at Corvallis, Oregon. These consisted of the correlation of weather conditions with the appearance of spore stages and waves of infection following critical periods of weather change.

In the greenhouse, the work involved principally the inoculation of Cuthbert red raspberries with spores. These inoculations were conducted under conditions of controlled temperature and humidity by the use of humidity chambers built for such purposes. These chambers were of two types. One consisted of a large enclosed chamber with a glass roof which allowed the passage of light. Dewpoint was maintained
by use of a heat element immersed in a container of water, and by draping with wet sheeting. The other type was a canvas tent enclosed within a glass box. A very fine spray of water played over the outside of the tent and produced a moisture-saturated atmosphere within. In most cases there were uninoculated check plants along with the inoculated ones. All plants were grown in the greenhouse, and before inoculation were subjected to twelve hours in the humidity chamber. Unless otherwise specified below, they were again subjected to these conditions for seventy-two hours after inoculation. This proved to be sufficiently long to give the desired results. Inoculations were made in various ways as designated in the descriptions of experiments.

The usual laboratory technique was used for study of the structure and function of the organism. The fresh leaf tissue was gathered from plants infected both in the field and greenhouse. Kraus' formalin-acetic-alcohol solution was the killing and fixing agent used. This particular solution was employed because it permits storage of the fixed leaf sections. A certain amount of difficulty was experienced in securing a stain that would differentiate the rust mycelium and nuclei from the host tissue. Chamberlains B method of using Flemming's triple stain proved the most satisfactory. All sections were cut from three to four, and never more than five, microns thick. The prepared slides were then studied in detail. Essential drawings
and photographs of these details are included below.

PYCNIA

Field observations. - As early as March 15th, 1931, leaves of the Cuthbert red raspberry had made their appearance at the base of last year's canes. On the ground and just underneath these new leaves were found the dead leaves of the previous season which harbored the overwintering sooty, black masses of teliospores. These spores form the initial source of infection that produce the pycnial stage on the newly developing leaves.

On March 25th pycnial infections were first recognized on the new leaves at lower levels of the canes in the field. These were in close proximity to teliospore masses, and were especially abundant where dead leaves were concentrated. This first infection period was preceded by a period of very prolonged wet weather and a moderate temperature.

Externally, pycnia are recognized as a very minute, pale-yellow, conical-shaped blisters on the surface of the leaf, particularly on the upper surface. These occur singly or in small groups. A mature pycnium measures from 40u. to 90u. in diameter and from 30u. to 35u. in height. A shiny glistening appearance is characteristic of the surface of the pycnium. This is caused by a thin film of moist exudate which contains pycniospores. Pycniospores are light, yellow
to brownish in color, have a granular content, and are uninucleate. They vary in size and shape, but are generally ellipsoid to globose, 2 - 3.6μ long by 0.5 - 2.0μ broad.

**Greenhouse experiments.** - Two experiments were performed to determine the time after teliospores were placed on the leaves until the first appearance of pycnia under greenhouse conditions. Potted plants were inoculated with teliospores which were secured from dead leaves in the field on March 25th, 1931. The inoculated plants were then placed in the humid chamber for 72 hours. In one case the pycnia made their first appearance in a period of 10 days, while in the second case there was a lapse of 13 days after inoculation.

From the field observations and the results obtained in the greenhouse experiments it was seen that sporidia must infect the new leaves in the spring as soon as the leaves make their appearance. As is pointed out later in this paper the teliospores germinate to produce sporidia only after a considerable rest period. If teliospores have had a sufficient rest period and occur in considerable abundance infection from sporidia will appear on the new leaves in from 10 days to two weeks. A period of high humidity or precipitation coupled with moderate temperature is conducive to initial infection. (See Table I).

**Histological studies.** - Stained vertical sections of leaf tissue were made to determine the origin and structure of the pycnia within the host. (See Plate XV, XX).
Pyenia, although most abundant above were found on both the upper and lower surfaces of the leaf. The germination of sporidia was not actually observed.

Pyenia develop from a thin pseudo-parenchymatous layer of mycelium which forms between the epidermis and the palisade layer of leaf cells and thus forces the two layers to separate. Vertical hyphae arise from this pseudo-parenchymatous layer to form thick palisade-like groups which find their way between the epidermal cells and tend to isolate the latter. Above the epidermis these hyphae begin to converge into a hemispherical mass, sometimes surrounding isolated epidermal cells, but the whole surmounted by the cuticle of the leaf. A general vertical section of a group of pyenia usually show several groups of hyphae separated by isolated, individual epidermal cells. These surrounded epidermal cells do not collapse as a rule. Within them and the palisade cells can be observed numerous haustoria of the fungus. The thin layer of cuticle, encountered in the upward progress of a developing pycnium becomes stretched and shiny. At maturity the cuticle is ruptured by the united force of the hyphae and the opening allows the dispersal of pycniospores.

An individual pycnium does not have any definite limiting peridial structure nor paraphyses. The terminals of the converging masses of hyphae mentioned above produce pycniospores near the place where the cuticle ruptures. The depth
of mature pycnia from the palisade cells of the host to the point of rupture is about 48u., and the widths vary from 60 to 370u.

The upward tapering hyphae or sporophores are septate and the cells are uninucleate. The single nucleus in each cell appears large and granular and is without a nucleolus. Some were found to be in the process of division, forming daughter nuclei. One of these migrates into the newly-formed pycniospore. These uninucleate spores are abstricted successively from the tips of the sporophores.

The pycniospores accumulate in quantity at the rupture of the cuticular layer and on the surface of the host leaf near the opening.

Microscopic studies were made of the nuclear condition of the pycnial stage, but nothing was found to indicate any connection with initiation of the binucleate condition found later in theaecium. There are, however, some points of significance. The presence of an exudate which contained pycniospores deserves further study to determine whether the function of the pycniospores of Phragmidium Rubi-Idaei is similar to that of certain species of Puccinia studied by Craigie. (8, 9).

The pycnium is always uninucleate and the sporidium that initiates it must also be uninucleate. To get the binucleate aecium there must be a fusion sometime after the pycnium is formed. The pycnia always mature and rupture
before the surrounding aecia are initiated, and no aecium forms independent of the encircled pycnia. Whether some pycnia will form without producing aecia is still an open question.

**AECIA**

**Field Observations.** - After the first appearance of pycnia on March 25th, a record of progress in the advance of aecia was maintained. Three Cuthbert red raspberry bushes were selected in the field. These plants were selected at a place in the row where the initial number of pycnia per unit area of leaf surface was closest to an average for the whole row. Eight leaflets were tagged on each plant. These leaflets were then watched at intervals of seven days, and a count was taken at each interval by checking a square centimeter of the upper surface at several points on each leaflet. This was accomplished by means of a piece of cardboard through which was cut a hole one centimeter in area. This cardboard was placed against the surface of the leaflet while the aecia were counted. The number of aecia were totaled and divided by the number of counts made. This gave an approximate average of the number of infections per square centimeter of surface in that particular region.

After May 7th, a new set of eight leaflets were selected from each of the bushes in the same locations, and a new count was started. This was done because sori of the first
set were not producing new infections. Infection for that particular wave had reached its peak.

The first appearance of infection on the leaf surface at any time was considered as the immature stages of the aecia. No separate records were made of immature and advanced infections, but an estimate was made of those aecia which had ruptured the epidermis of the leaf. On the whole row of bushes notes were also kept to indicate the advance of aecia to higher levels from the ground.

Table I presents in tabulated form the data on waves of aecial infections in the field. Plates I and II show a graphical correlation between the relative humidity, rainfall in inches, and temperature, and the progress of aecial infection. The meteorological records were secured from the local weather station at Corvallis, Oregon. All the field records were taken three miles east of the city.

A study of the data in Table I will show that there was a steady increase in the number of aecia which reached a maximum on May 7th. From that time there was a slow advance in the number of aecial sori. The period from March 1st to April 14th was a period of more or less continuous heavy or light rainfall and relatively high humidity at frequent intervals. The temperature stayed well below 70 degrees F. It seems evident that the heavy rainfall previous to April 14th was responsible for the rapid increase in the number of aecia between March 25th and May 7th.
Table I

Showing waves ofaecial infections
during the spring of 1931

<table>
<thead>
<tr>
<th>1931</th>
<th>Infections, average per sq.cm.of leaf surface</th>
<th>Percentage of mature sori</th>
<th>Height of infections from ground (inches)</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaves exposed to first infection wave</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mar.25</td>
<td>.2</td>
<td>None</td>
<td>0--8</td>
</tr>
<tr>
<td></td>
<td>Apr.2</td>
<td>1.4</td>
<td>None</td>
<td>0--8</td>
</tr>
<tr>
<td></td>
<td>Apr.9</td>
<td>3.9</td>
<td>10%</td>
<td>0--8</td>
</tr>
<tr>
<td></td>
<td>Apr.16</td>
<td>4.6</td>
<td>50%</td>
<td>8--30</td>
</tr>
<tr>
<td></td>
<td>Apr.23</td>
<td>6.2</td>
<td>75%</td>
<td>8--30</td>
</tr>
<tr>
<td></td>
<td>Apr.30</td>
<td>7.</td>
<td>90%</td>
<td>30--60</td>
</tr>
<tr>
<td></td>
<td>May 7</td>
<td>8.2</td>
<td>100%</td>
<td>50% Mature, All levels</td>
</tr>
<tr>
<td></td>
<td>Leaves exposed to second infection wave</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>May 14</td>
<td>.0</td>
<td>None</td>
<td>75% Mature All levels</td>
</tr>
<tr>
<td></td>
<td>May 21</td>
<td>.1</td>
<td>25%</td>
<td>80% Mature, All levels</td>
</tr>
<tr>
<td></td>
<td>May 28</td>
<td>3.4</td>
<td>50%</td>
<td>90% Mature, All levels</td>
</tr>
<tr>
<td></td>
<td>June 3</td>
<td>4.0</td>
<td>100%</td>
<td>100% Mature, First uredinia appeared</td>
</tr>
</tbody>
</table>
PLATE I.
MARCH

APRIL

MAY

RELATIVE HUMIDITY

RAINFALL
IN INCHES

TEMPERATURE
DEG. F.

AERIAL INFECTION
AVE. NO. PER SQ. CM.

MAXIMUM

MINIMUM

GRAPHIC FIELD RECORD OF YELLOW RUST OF RUBUS AND ITS RELATION TO WEATHER

CORVALLIS, ORE., 1931
PLATE II.
GRAPHIC FIELD RECORD OF YELLOW RUST OF RUBUS AND ITS RELATION TO WEATHER

CORVALLIS, ORE., 1931
After this time aecial infections showed a slow increase, reaching and maintaining a rather level maximum in the plot studied. There were scattered aecia at other points in the field, but generally they were all mature by May 7th.

According to the weather records, there was no rainfall from April 15th to April 30th. There was also a rapid decline in humidity and an increase in temperature which reached a maximum of 84 degrees F. on April 27th. During the first three days of May there was a slight amount of rainfall, an increase in humidity, and a drop in temperature. This perhaps accounts for the second wave of aecial infections which show in Table I and Plate II between May 14th and June 3rd. Somewhat the same climatic conditions of humidity, precipitation, and temperature were duplicated on May 15th to 17th, which doubtless augmented the rise in the curve of aecial infections between May 21st and June 3rd.

From these records it seems reasonable to believe that teliospore germination and subsequent infection by sporidia had materially decreased after the rains previous to April 15th. The rain from May 1st to 3rd did not promote excessive aecial infection as the tables show, but augmented by the rain on May 15th to 17th, the teliospores were stimulated again.

There is a gradual increase in numbers of aecia at higher levels on the plants as they produce leaves at these elevations from the ground, but the greatest aecial concentration is confined to the leaves near the ground. Both
petioles and young canes show aecial infections during the second wave of infections by sporidium (May 21st to June 3rd). These are earlier cane lesions than those reported by Zeller (26), who reported only uredinial lesions on canes.

The single aecial sorus of Phragmidium Rubi-Idaei at first presents a raised circular, minute, light yellow, blister. These developing aecia finally burst through the epidermis of the leaf to expose a tufted circle of clusters of aeciospores around a depressed smooth center which supports what remains of the pycnia. (See Plates VII and XIV, B). A mature sorus measures from $\frac{1}{4}$ to 1 mm. in diameter. The aeciospores are sub-globose to broadly ellipsoid or ovoid, 15.5 - 23.8 x 14.6 - 21.9 u. in size. The outer surface has pale yellow broadly conic and sharply papillose walls. (See Plate XVIII, B) The papillae are from 1 to 1$\frac{1}{2}$ u. long. Walls, in cross section, are 1.5 to 2 u. in thickness. The thick wall is called the exospore.

**Greenhouse Experiments.** - Several observations of infection of the Cuthbert red raspberry were made in the greenhouse. The plants were inoculated with teliospores and the production of pycnia and aecia were noted from time to time. One experiment was made to determine whether germination of teliospores could be induced through direct application of spores on the leaves of the host. Another experiment was performed to show whether infection could be produced on either the upper or lower side of the leaf.
29th dead leaves infected with teliospores were taken from the field near Corvallis, Oregon. The teliospores were transferred to the leaves of a healthy plant in the greenhouse. Three different groups of leaves were selected so as to be well isolated from each other. The first group was inoculated on the lower surface, the second on the upper surface, and the third was an uninoculated check. The plant was then placed in the humid chamber for 72 hours at a temperature of 26 degrees C., and 100% atmospheric humidity.

On February 13th or 14 days later, pycnia had made their appearance on the leaves which had been inoculated. Pycnia appeared only on the upper surface of those leaves inoculated on that surface and only on the lower surface of those inoculated below. By February 18th immature aecia had formed, and by February 26th, aecia had reached maturity. Out of nine leaves examined from each group, on those inoculated on the lower surface, there were ninety mature aecial sori, and on those inoculations made on the upper surface there were eighty-one.

The results showed such slight differences between the inoculations made on the upper and lower sides of the leaves that it was concluded the sporidia from teliospores could infect either the upper or lower sides of the leaf about equally well, and that probably stomata have no bearing on the penetration of the germ tube into the leaf tissue. Stomata are rarely found on the upper surface of the
Cuthbert red raspberry, but aecia are usually found more abundantly on the upper side of leaves. From the greenhouse experience it would seem, therefore that sporidia shot into the air more often alight on the upper surface of leaves than do they adhere the lower surfaces.

If an inoculated plant was placed under a bell jar and provided with a saturated moisture-atmosphere, it was possible to obtain initial stages of infection in seven days, immature aecia in ten days, and mature aecia in about fourteen days after inoculation.

Another experiment was prepared to determine whether teliospores suspended above a plant and not in direct contact with the leaves would produce infection. Two healthy plants were each enclosed in separate cylindric wire nets. A wire screen platform was placed above each plant. On the platform above one plant was placed a layer of moistened, dead leaves which contained viable teliospores. This plant was then placed in the humid chamber for 120 hours. The other plant was treated in a similar manner, but was not put into the humid chamber. The dead leaves, however, were kept in a moistened condition in both cases.

After taking the first plant out of the humidor, a careful watch was kept to note any signs of infection on either plant. Nothing developed on the first plant which had been kept in the humid chamber, but the one that had been kept under greenhouse conditions showed aecial infection on two
leaves. These leaves, however, were in such a position that water dripping from one side of the source of inoculum fell directly upon them. Infection was obtained also when the first plant was again placed in the humid chamber and water was allowed to drip upon certain of the leaves. Microscopic examination of the leaf surface did not show any teliospores on the leaves infected. It would seem from these results that sporidia were washed or drifted down on to the leaves and germinated in the presence of free water. A humid condition alone with wet or soaked teliospores would not induce infection on the leaf when the source of inoculum was at a distance. Free water on the leaf surface seems essential for germination of the sporidia. In the field aecia are found as high as three feet or more from the source of infection on the ground. It is probable that sporidia are wind borne to the leaves, and with free moisture present, will germinate.

**Histological Studies.** - In the histological studies of the aecium of *Phragmidium Rubi-Idae* an attempt was made to compare as much as possible the sexual mechanism found in this species with that described by other workers who have studied species of Phragmidium. Finer details of a thorough cytological study were not attempted in this investigation.

Vertical sections of raspberry leaves harboring aecial infections were prepared in permanent histological mounts.
These show that the aecial scorus is of the ceoma type, in that it lacks a peridium. The manner of initiation and maturation of the aecium seems to correspond quite closely in detail with those species of Phragmidium described by Blackman (4), Wellsford (15), and Christman (6). The review of their work in this connection is given in the supplement to this thesis.

The primordium starts as a layer of uninucleate hyphae which is two to three cells thick and lies just below the epidermis. This layer is continuous with the primordial hyphae which were originally laid down at the initiation of pycnia. (See Plate XX,A). The nuclei in these hyphae are small and dense. Just above these hyphal cells are formed a series of perpendicular cells. (See Plates XI,A and XIX,A). Some contain a single nucleus, while others are distinctly bi-nucleate. In all cases the nuclei were large, and were composed of a clear chromatin network. This seemed to indicate that they were in their active stages. The exact point of attachment of these cells was not definitely established.

Later stages of development show that division has taken place to form a series of perpendicular, elongated cells in chains. The so-called buffer cells which rapidly disintegrate are found at the distal end. At this stage, several characteristic fusion cells described by Christman (6) were apparent. (See Plate XIX,A) Where distal cells
of these perpendicular hyphae come in contact, the walls disappear at the point of contact and the contents of the one cell appears continuous with the other. Neither a migration or division of nuclei was observed, but a single nucleus was found in each cell close to the opening. According to Christman, these two nuclei come to lie side by side at the point of junction of the two cells, and each divides. One daughter nucleus from each wanders back into its respective cell, and the other two move into the distal end of the fused cell part, and are cut off by a cell wall.

Although there are several of these so-called fusion cells present in some sections of immature aecia, there are also many more binucleate cells which do not appear as fusion cells. Whether these are the result of earlier fusions is yet an open question. It is sufficient to say that at the apex of all the binucleate basal cells are formed first a binucleate intercalary cell and above that a young aeciospore. The basal cell elongates and the process is repeated until the mature aecium presents a series of basal cells producing a chain of aeciospores alternating with intercalary cells. The intercalary cells later disintegrate and the aeciospores are dispersed. (See Plate XIX,A and B).

Paraphyses are formed in the early stages of aecial development and finally exceed the height of the spore mass. They arise from uninucleate hyphae at the base of the aecium. By the time of aeciospore formation they have become a fringe
of elongate, clavately-incurved, sterile cells, encircling each aecium. A mature aecium, with its paraphyses, measures approximately 165 u. in diameter. Each sorus rises above the surface of the leaf, and consists of a circle of aecia with incurved paraphyses surrounding several pycnia (See Plates XII and XV, A).

UREDINIA

Field Observations. - Uredinia were first noticed in the field on May 28th, 1931, and from that time a record was kept of their progress. The same bushes were chosen for observation as those on which the aecia had been previously observed. This was done because they represented a location where heavy aecial infection had taken place. Leaflets that had made their appearance at about the time of heaviest aeciospore dissemination, were tagged and the appearance of uredinial infections were noted thereafter. The method chosen for counting was similar to that used for the aecia. Ten leaflets were tagged on each plant. After the first wave of infection and maturity of uredinia, another set of younger leaflets were chosen and treated in a similar manner. This system was repeated through the summer from May 28th to October 8th, during which period there were four waves of infection. This gave accurate check on the different waves of infection and their severity. The number of uredinia per square centimeter of leaf
surface was recorded for each week, for the most part, and are indicated in Table II. A correlations of these waves of uredinial infections produced by *P. Rubi-Idaei* with meteorological data on precipitation, temperature, and relative humidity for the period, are presented graphically in Plates III, IV, and V.

A glance at the graphic representations will show that there were four definite waves of uredinial infections appearing in the field during the spring, summer, and fall of 1931. The initial wave started on about May 28th and advanced slowly to June 24th. (See Plate II) It must have been caused principally by infections from aeciospores. Infections were scarce on the plot as a whole. This initial wave was doubtless brought about by the rainfall and slight rise in humidity which took place between May 15th and May 18th and the favoring higher temperatures from May 30th to June 4th.

From May 18th until June 8th there was no precipitation. The temperature rose to 90 degrees F. and there was a decided drop in relative humidity. Had there been more rainfall between May 18th and June 8th it is probably that the initial wave would have been much heavier as a whole, but under the circumstances the curve of infection did not rise perceptibly.

The heaviest spring rains in this locality for 1931 started on June 9th, and continued until June 29th, reaching
Table II

Showing waves of uredinial infections
during the spring and summer of 1931

<table>
<thead>
<tr>
<th>Year</th>
<th>Infections</th>
<th>Average per sq. cm. of leaf surface</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leaves exposed to first infection wave</td>
<td></td>
</tr>
<tr>
<td>May 28</td>
<td>5.6</td>
<td></td>
</tr>
<tr>
<td>June 3</td>
<td>6.2</td>
<td></td>
</tr>
<tr>
<td>June 10</td>
<td>6.4</td>
<td></td>
</tr>
<tr>
<td>June 17</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>June 24</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leaves exposed to second infection wave</td>
<td></td>
</tr>
<tr>
<td>July 2</td>
<td>18.3</td>
<td>First Telia</td>
</tr>
<tr>
<td>July 9</td>
<td>32.7</td>
<td>Increased Telia</td>
</tr>
<tr>
<td>July 16</td>
<td>40.4</td>
<td></td>
</tr>
<tr>
<td>July 23</td>
<td>Leaflets covered</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leaves exposed to third infection wave</td>
<td></td>
</tr>
<tr>
<td>July 30</td>
<td>.0</td>
<td>Increased Telia</td>
</tr>
<tr>
<td>Aug. 6</td>
<td>4.3</td>
<td></td>
</tr>
<tr>
<td>Aug. 13</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>Aug. 20</td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td>Aug. 27</td>
<td>6.1</td>
<td></td>
</tr>
<tr>
<td>Sept. 3</td>
<td>6.4</td>
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</tr>
<tr>
<td>Sept. 10</td>
<td>6.4</td>
<td></td>
</tr>
</tbody>
</table>

(Continued)
<table>
<thead>
<tr>
<th>Date</th>
<th>Infections</th>
<th>Leaves exposed to fourth infection wave</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept. 17</td>
<td>1.1</td>
<td>Increased Telia</td>
</tr>
<tr>
<td>Sept. 24</td>
<td>2.3</td>
<td>&quot;</td>
</tr>
<tr>
<td>Oct. 1</td>
<td>3.8</td>
<td>&quot;</td>
</tr>
<tr>
<td>Oct. 8</td>
<td>3.9</td>
<td>&quot;</td>
</tr>
</tbody>
</table>
PLATE III.
GRAPHIC FIELD RECORD OF YELLOW RUST OF RUBUS
AND ITS RELATION TO WEATHER
CORVALLIS, ORE., 1931
PLATE IV.
GRAPHIC FIELD RECORD OF YELLOW RUST OF RUBUS AND ITS RELATION TO WEATHER

CORVALLIS, ORE., 1931
GRAPHIC FIELD RECORD OF YELLOW RUST OF RUBUS
AND ITS RELATION TO WEATHER

CORVALLIS, ORE., 1931
its height on June 17th. The heaviest uredinial infections for the year appeared between July 2nd and July 23rd and reached a point where the under sides of the leaflets were completely covered with yellow masses of urediniospores. This constitutes the second and most severe wave of uredinial infections. The bulk of these infections were initiated by the first wave of urediniospores and probably by scattered aeciospores. Intermittent periods of high humidity and moderate temperatures assisted materially in spore germination and infection.

Both the third and fourth waves were small and gradual. The third, which began on July 30th was induced by a slight precipitation on July 13th. The fourth was accelerated in a similar manner by intermittent rains and high humidity during the first and middle parts of September.

It is of interest to note that there is a lag of several days between the period of precipitation and infection waves in both the production of aecia and uredinia.

Telia first made their appearance on about July 2nd and gradually replaced the uredinia which gradually disappeared.

From an analysis of these data it can be seen that waves of uredinia in the field depend entirely upon the amount of rainfall and relative humidity that takes place during the spring and summer. A heavy continuous rainy spell during the summer of 1931 would undoubtedly have resulted in
more than one heavy wave of uredinial infection.

Uredinia are found in lesions on the underside of the leaf, and on the petioles and new canes. Leaf infections cannot readily be recognized by the unaided eye in the early stages of development of uredinia in the leaf tissue. About the time of rupture on the underside of the leaf, small light yellow pin-head dots can be seen through on the upper surface. These enlarge to about 0.5 mm. in diameter to form yellow-brown necrotic spots which may coalesce to involve from 50 to 75% of the leaf surface. On the underside are the pustules which begin as minute light yellow or yellowish white tufts of urediniospores. Each gradually enlarges to about 0.1 to 0.2 mm. in diameter to form a rounded mass.

The lower surface of a heavily infected leaf may have a mass of yellow spores covering it, with the separate uredinia indistinguishable. (See Plate IX).

Lesions on stems are usually elliptical and produce a small canker which may measure as large as 1½ cm. long by ½ cm. wide. An examination of these shows that they are composed of a mixture of pycniospores, aeciospores, and urediniospores.

Urediniospores differ from the aeciospores in being more or less ellipsoidal to almost ovoid in shape. The outer surface is papillose, with the papillae narrow-conic, and from .7 to 1 u. long. These papillae are about 1½ times as numerous as those on the aeciospores. (See Plate XVIII). The
walls are light yellow and 3/4 to 1 u. thick. Spore sizes range from 13.9 - 19.4 u. wide by 13.5 - 20.3 u. long.

Uredinial infections produce a greater necrotic effect on the host than do the aeciospores. In some places along a row of raspberry bushes heavy concentration of uredinia will show a marked reduction in functioning foliage, while other places in the same row show little or no damage. When uredinia are numerous on the lower surface of the leaves their influence on the vitality and immediate tissues of the leaf shows through to the upper surface, as shown in Plate VIII.

Greenhouse Experiments. - Greenhouse experiments involved inoculations of Cuthbert red raspberry plants with aeciospores and urediniospores. One of these was undertaken to determine the period that lapses between aecial inoculation and the appearance of uredinia. It was also desirable to know whether aeciospores will produce infections when applied to either the upper or lower surface of the leaves separately. Another experiment was designed for a similar purpose, except that the initial inoculations were with urediniospores.

Three healthy potted Cuthbert red raspberry plants were chosen for the first test. Viable aeciospores were secured from the field and transferred to the leaf surfaces by means of a camel's-hair brush. The leaf surfaces had been previously atomized with distilled water to provide moisture. One plant was inoculated on the upper surface only, and the other on the lower surface. The third was left uninoculat-
ed as a check. All three plants were put in the humid case for 72 hours at 100% relative humidity and at 78 degrees F.

Sixteen days after inoculation, uredinia made their appearance on the plant, leaves of which had been inoculated on the underside. The plant having leaves inoculated on the upper side did not produce uredinia. The experiment seemed to indicate that aeciospores will infect only on the underside of the leaf. Later studies have shown that uredinia always occur directly below stomata. We can therefore assume that aeciospores infect through stomata and uredinia occur more frequently on the lower surface of leaves because of the abundance of stomata on that side. The period between infection and maturation of uredinia varied from eight to twelve days.

It was found that by using urediniospores as the source of inoculum in the second experiment, uredinal infections could be produced only on the underside of the leaf. The first uredinia appeared in thirteen days after inoculation and maturity of uredinia occurred in thirteen or more days.

The two experiments show that aeciospores and urediniospores infect only on the underside of the leaf, that inoculations with aeciospores will produce uredinal infections in about sixteen days, and that inoculations with urediniospores will produce secondary urediniospores in about thirteen days.

Histological Studies. - It has already been demonstrat-
ed in this study that urediniospores infect only the underside of a leaf and only through stomata. It is obvious that only those spores which fall upon a stomata produce infection, or that a more distant spore must form a germ tube on the underside of the leaf and this germ tube grows to and infects through a stomate. Just how this stage of infection is accomplished was not studied. Sections of leaf tissue showing stages of germination of spores were not made, but sections of all stages in uredinial formation did show that infection had taken place only at the stomatal openings.

The sorus begins with a binucleate primordium consisting of a few small mycelial hyphae in the substomatal cavity and just below the layer of spongy mesophyll tissue of the leaf. From this primordium, perpendicular, elongated, basal cells extend downward. (See Plate XVII,B). Each basal cell cuts off an initial cell at its distal end. This distal cell further divides to form the pedicel and spore. (See Plate XI,B). Several initials may develop from one basal cell. The pedicel or stipe is moderately thin, and about twice the length of a spore. With the increased production of basal cells, pedicels, and spores, the mature sorus becomes compact at the base and spreads out towards the apex. The spores and pedicels lie well above the ruptured epidermis. These various characters of the mature uredinium are shown in Plates XII,B and XVII,A.

A thin layer of somewhat incurved, club-shaped para-
physes encircle each sorus and extend well above the spores on their pedicels. Stained vertical sections of mature uredinia vary in size, but usually they range between 83.3 to 153.4 μ. in diameter and 58.6 to 80.5 μ. in height from the tips of the paraphyses to the bases of the initial cells.

After the urediniospores become mature, they are released from their pedicels and are disseminated in masses on the surface of the leaf.

All cells of the uredinium have originated from the germination of a binucleate spore and in turn they all contain two nuclei. The nuclei are smaller in size, and do not seem to contain as rich a chromatin network as that found in the nuclei in the aecium.

Since, as pointed out later under the discussion of telia, the telium occurs in the same sorus and from the same infection by an aeciospore which produces the uredinium, it might be assumed that the uredinium is rather an unnecessary stage in the life history of this species of rust, except that it does increase the number of uredinia and telia through additional waves of secondary infection.

**TELIA**

**Field Observations.** - Teliospores were first observed in the field on July 2nd, 1931. They make their occasional appearance in the same sorus with urediniospores. Later they are found arising as clusters in separate sori which are composed of teliospores only. The period from July 2nd
to September 5th was one of very dry weather in which urediniospores were being replaced by thick clusters of teliospores. By October 4th urediniospores had practically disappeared, and all leaves which had been infected for some time were covered with black clusters of teliospores. These leaves fall to the ground where the attached spore masses lie dormant through the winter. In early spring, under favorable conditions of moist weather, they germinate producing sporidia which initiate infections which produce pycnia and aecia on the first developing leaves and canes.

Telia are scattered on the leaf, but in some places are found blended with heavy infections of urediniospores. (See Plate VII). The single telium which arises directly from infection by a urediniospore consists of only a few naked projecting spores at first, and under a hand lens appears more or less nut-brown in color. At maturity they become blackened by a large group of teliospores. The diameter of the telial pustules is from 2.5 mm. to 8 mm.

Teliospores of Phragmidium Rubi-Idaei are cylindrical, 26 - 35 u. x 65 - 120 u. and are rounded below. A blunt, conical, hyaline apiculus is found at the apex of each spore. (See Plate XVIII, A). These are generally from 1 to 10 u. long (rarely less than 4 u.). A count of the average number of cells within each spore indicates that the majority of them are from 6 to 7 celled, but the range runs from 5 to 10. Rarely are there more than 8 cells in each spore. The
walls are dark, chocolate-brown, and closely and rather coarsely verrucose. The pedicels are rugose when removed from dry leaves, and are from 70 to 117 u. long. Both the upper and lower portions are colorless except near the spore. The upper portion is from 9 to 10 u. in diameter and the lower swells in water to claviform and is from 14 to 27 u. in diameter. These measurements and descriptions correspond quite closely with those of Arthur (1) and Zeller (16).

Specimens of teliospores on Rubus Idaeus from England were compared with specimens on Rubus strigosus (Cuthbert variety) from Oregon. They appeared to be identical in all respects.

**Histological Studies.** - It has been previously demonstrated in this study that teliospores from the field could be germinated on the living plant in the greenhouse as early in the winter as January 29th. Several attempts to germinate teliospores artificially in hanging drops, or in glass covered humid chambers failed to give results earlier in the autumn even under various temperature conditions. However, a small percentage of teliospores taken from the field about March 14th, germinated in hanging drops. This indicates that before germinating, teliospores of P. Rubi-Idaei must have a considerable rest period and perhaps atmospheric temperatures which are at least as low as prevail in winter under Western Oregon conditions. At the same time
difficulty was experienced in obtaining germination of teliospores in water. Teliospores placed on leaves in the greenhouse germinated much more readily. Evidently the host must have some stimulating influence on teliospore germination.

It was possible, with hanging drops under laboratory temperature, to secure a long, narrow, mycelium-like germ tube from each of several cells in many of the teliospores. The cells from which these arose became much more translucent than those that produced no germ tubes. This tube or promycelium is sometimes as much as from 4 to 5 times as long as a 6-celled teliospore. It is composed of clear, vacuolated spaces surrounded by a light brown, granular pigment. The wall is thin, and if septation is present, it was not easily distinguishable. Germ pores are indistinct in the teliospore walls. It was therefore impossible to ascertain whether the tube finds its way to the outside through such an outlet.

Blackman (4) described these promycelia in his work with Phragmidium violaceum. In connection with his studies of the nuclear mechanism in the teliospore, he mentions a spherical mass of yellow cytoplasm welling out through one of the pores of a teliospore cell. After the nucleus of the cell has increased in size, it passes into the germ tube through the cell pore. In water medium, where the germ tube does not reach the air, it continues to grow and the nucleus
and protoplasm of the empty cell are found at the end of the tube.

He further shows that a promycelium, growing under water, develops to a great length without dividing or forming sporidia. In some cases the promycelium had divided into four cells under water, and one of these four cells put out a germ tube. He concluded that in Gymnosporium and Phragmidium (P. violaceum) the real germinating unit is the promycelial cell, and that under certain conditions it is capable of becoming a separate spore, put out a germ tube, and act as a sporidium in causing infection. He mentions the work of Sapin-Trouffy on Phragmidium malvacaerum. In this rust submerged promycelial cells separated and put out branch hyphae which became sterigmata and bore spores only when they reached the air.

No histological work was undertaken in the study of the germination of teliospores of P. Rubi-Idaei, but the germ tubes described by Blackman were identical with germination in water observed by the writer.

It seems reasonable, by comparison, that we have a condition in Phragmidium Rubi-Idaei similar to that observed by Blackman in P. violaceum. There is therefore the probability of two modes of initial infection by teliospores namely; (1) by means of a teliospore and direct infection, and (2) by means of sporidia from a remote teliospore.

As was previously stated in this paper teliospores were
seen to arise from either uridinial sori or from sori which were devoted to the production of teliospores only. Teliospores were also observed to come from independent telial sori produced directly from infections by urediniospores. Vertical sections taken of the leaf tissue seem to confirm these observations. In either event, teliospores arise from rectangular, binucleate, basal cells in a very similar manner to that of the urediniospores which preceded them. One, or more, elongate and binucleate cell pushes upward from each basal cell and enlarges. Some appear to be empty and sterile. They perhaps could be designated as paraphyses intermingled with the spore-forming cells.

Meanwhile the two nuclei within the spore-forming cells begin to divide and form several pairs of daughter nuclei. At about the same time, cells are cut off, from the apex downward, by horizontal cross-walls. Usually this results in a series of 5 to 8 short, superimposed cells. The upper cell projects slightly at its apex to form the hyaline apiculus. The lowest cell forms an elongated stalk which has a narrow cavity above which broadens into a larger cavity below. The teliospore detaches itself below the stalk, which is always considered as part of the spore. When the spore is detached from its basal cell, the stalk base is shown to be swollen immediately above the point of attachment. Some evidence of a circular shield at the point of cleavage was noted. As the spore matures, the walls of
35.

each cell become thickened and dark colored, and the pair-
ed nuclei within each cell fuse to form a large fusion
nucleus. Those in the stalk disintegrate. These conditions
are illustrated in Plates XIII, XVI, and XVIII,A.

HOSTS

VARIETAL SUSCEPTIBILITY

When studies relating to this rust were first proposed,
there was seen the need for an experiment which would pro-
vide information regarding the susceptibility of different
available varieties of the host plants. Previous references
to the disease report it as having been found in America on
Rubus leucodermis Douglas (Western Wild Black raspberry),
Rubus occidentalis Linn, (Black raspberry), Rubus strigosus
Michx. (Red raspberry), and Rubus spectabilis Pursh (Salmon
berry). (1) (16)

In Europe, according to Grove (12) Rubus Idaeus Linn.
(European raspberry) and other species of Rubus are suscept-
able. Saccardo (13) mentions it as found on Rubus strigosus.

During the fall and winter of 1931-32, greenhouse ex-
periments were performed to determine to some degree the
ranges of susceptibility of the available species and variet-
ies of Rubus and also of three species of Rosa.

The following species and horticultural varieties of
Rubus were tested for susceptibility: - (1), twelve horti-
cultural varieties of red raspberries as follows, Antwerp,
Cayuga, Chief, Cuthbert, Golden Queen, Herbert, Latham, Lloyd George, Marlboro, Owasco, Ranere or St. Regis, and Seneca; (2), three horticultural varieties of \textit{R. occidentalis} as follows, Cumberland, Munger, and Plum Farmer; (3), the purple cane raspberry, Webster; (4), eight horticultural varieties of blackberry as follows, Cory-thornless, Himalaya, Kittatiny, Lawton, Mammoth, Phenomenal, Stewart, and Youngberry; (5), the loganberry (\textit{Rubus loganobaccus}); (6), the two wild blackberries, \textit{Rubus laciniatus} (Evergreen blackberry), and \textit{Rubus ursinus} (the training blackberry and the selection of it known as Ideal Wild); and (7), three other native species of Rubus, as follows: Western wild black raspberry (\textit{R. leucodermis}), Salmon berry (\textit{R. spectabilis}), and Thimbleberry (\textit{R. parviflorus}). The species of \textit{Rosa} tested were \textit{Rosa gymnocarpa} Nutt., \textit{Rosa nutkana} Presl., and \textit{Rosa rubiginosa} L.

All plants used in this experiment were first transferred from the field to the greenhouse where they were potted and allowed to develop before being subjected to treatment. The plants were then divided into sets of from ten to twelve varieties each, and each set was provided with one Cuthbert red raspberry plant which was known to be susceptible. This acted as a means of comparison. Each set was treated separately and carried through to completion before the next one was started. A humidity chamber capable of providing a saturated atmospheric condition and a temperature of from 68-70 degrees F. was used. The chamber was large enough to accommodate one set at a time. Each set was always subject-
ed to 24 hours of humid atmosphere before inoculation, and was inoculated immediately thereafter with urediniospores which had been cultured on Cuthbert red raspberry plants grown in the greenhouse. These spores were used as the source of inoculum for all sets and were perpetuated in this manner by a continuous transfer from one Cuthbert plant to another.

After the 24-hour treatment in the humidity chamber, the undersides of the leaves of each plant were thoroughly and equally sprayed with a concentrated suspension of urediniospores in distilled water by means of an ordinary atomiser. The plants were then given a 72-hour incubation in the humid chamber.

After removal, six examinations were made at the end of 13, 15, 19, 23, 28, and 32 days from the time of inoculation. Each set was treated similarly.

The procedure used in making the first four examinations consisted in determining the average number of infections per square centimeter of surface on nine tagged leaflets selected from each plant. This was done by using a series of measured cardboard pieces shaped to represent the average sizes of different leaflets. It was only necessary to count the number of infections on the underside of the nine leaflets and divide this by the total square centimeters of leaf surface as represented by the total area of cardboard pieces used. This gave the average infection per square centimeter.
During the first four examinations a check was also kept of the comparative sizes of the pustules on one plant against those of another because it was found that some varieties exhibited much larger pustules than others. Since the size of the pustule seems to indicate degree of vigor of the rust on the particular host it was felt that this factor should be taken into consideration when judging the degree of susceptibility of one plant over another. On the 28th day after inoculation, the appearance of telia was observed and a record of their relative abundance was noted. Finally, after 32 days, the general condition of each plant was recorded as based on the damage to the leaf tissue.

Three preliminary and two final sets were run. The preliminary sets separated the susceptible from the non-susceptible plants. Duplicate plants of the susceptible and non-susceptible varieties respectively made up the two final sets which were run separately as a check. All counts and general characters of the susceptible varieties were combined into one summary which is given in Table III.

In the first four columns "P" refers to the pustules and the letters under this column designate the comparative sizes of the pustules such as "L"--large, "M"--medium, "S"--small, "VS"--very small. The column marked telia refers to the degree of abundance of telia. The letter "H"--heavy, "M"--medium, "S"--slight, and "N"--none. The varieties are placed in the order of their susceptibility.
Table III.
Showing Relative Susceptibility of Certain Horticultural Varieties and Species of Rubus
as indicated by Greenhouse Tests - 1931

<table>
<thead>
<tr>
<th>Susceptible plants</th>
<th>Period of Examination after inoculation</th>
<th>Telia</th>
<th>Condition of Plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>13 days</td>
<td>15 days</td>
<td>19 days</td>
</tr>
<tr>
<td>Variety of Species</td>
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<td>inf.</td>
<td>inf.</td>
</tr>
<tr>
<td>sq.cm. P</td>
<td>sq.cm. P</td>
<td>sq.cm. P</td>
<td>sq.cm. P</td>
</tr>
<tr>
<td>Marlboro</td>
<td>12.4 L</td>
<td>19.4 L</td>
<td>65.6 L</td>
</tr>
<tr>
<td>Cuthbert</td>
<td>7.6 S</td>
<td>16.8 L</td>
<td>39.9 L</td>
</tr>
<tr>
<td>Rubus Leucodermis</td>
<td>2.8 S</td>
<td>12.7 M</td>
<td>31.9 L</td>
</tr>
<tr>
<td>Golden Queen</td>
<td>2.9 M</td>
<td>9.9 L</td>
<td>26.8 L</td>
</tr>
<tr>
<td>Webster</td>
<td>1.5 S</td>
<td>5.4 S</td>
<td>38.5 M</td>
</tr>
<tr>
<td>Herbert</td>
<td>1.1 S</td>
<td>2.3 M</td>
<td>11.7 M</td>
</tr>
</tbody>
</table>

For explanation of symbols see page 38.
Table III (Concluded)

<table>
<thead>
<tr>
<th>Susceptible plants</th>
<th>Period of examination after inoculation</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
<th>Variety or Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>13 days</td>
<td>15 days</td>
<td>19 days</td>
<td>23 days</td>
<td>23 days</td>
<td>32 days</td>
<td>Tilia Condition of Plant</td>
<td></td>
</tr>
<tr>
<td>Variety or Species</td>
<td>Inf. sq.cm. P</td>
<td>inf. sq.cm. P</td>
<td>inf. sq.cm. P</td>
<td>inf. sq.cm. P</td>
<td>Telia</td>
<td>Condition of Plant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cayuga</td>
<td>0.1 S</td>
<td>2.5 S</td>
<td>17.7 S</td>
<td>29.6 S</td>
<td>S S</td>
<td>Slightly affected; Spots yellowed.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranere or St. Regis</td>
<td>4.2 S</td>
<td>6.5 S</td>
<td>14.8 S</td>
<td>21.7 S</td>
<td>S M</td>
<td>Slightly affected; spots yellowed.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antwerp</td>
<td>3.6 S</td>
<td>6.1 S</td>
<td>5.4 S</td>
<td>18.4 S</td>
<td>S H</td>
<td>Slightly affected; spots lightly yellowed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seneca</td>
<td>0.0 -</td>
<td>0.0 -</td>
<td>2.5 S</td>
<td>17.7 M</td>
<td>S</td>
<td>Slightly affected; spots lightly yellowed.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Owasco</td>
<td>0.0 -</td>
<td>0.0 -</td>
<td>6.0 S</td>
<td>10.0 S</td>
<td>S N</td>
<td>Slightly affected; scarcely spotted.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cumberland</td>
<td>0.0 -</td>
<td>1.0 VS 2.8 VS</td>
<td>6.3 VS</td>
<td>N</td>
<td>Very slightly affected; Scarcely spotted.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lloyd George</td>
<td>0.0 -</td>
<td>0.0 -</td>
<td>3.5 VS</td>
<td>5.4 VS</td>
<td>N</td>
<td>Very slightly affected; scarcely spotted.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For explanation of symbols see page 38.
A glance over the table shows that Rubus leucodermis (western wild black raspberry) was very susceptible to the yellow rust as were also 12 varieties of (red raspberry). The purple cane variety, Webster, showed an average final infection 43.45 pustules per square centimeter, but an examination of the pustules and general condition of the plant tended to bring its susceptibility below either the western wild black raspberry or Golden Queen. In the final analysis of this variety, after the 32 day period, it was found to show a smaller percentage of necrotic spots than either of the other plants listed above it. It was therefore placed below the other very susceptible varieties.

The following species and varieties were found entirely resistant to yellow rust after duplicate tests had been made:

<table>
<thead>
<tr>
<th>Blackberry</th>
<th>Rubus strigosus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kittatiny</td>
<td>Chief</td>
</tr>
<tr>
<td>Youngberry</td>
<td>Latham</td>
</tr>
<tr>
<td>Himalaya</td>
<td>Rubus spectabilis</td>
</tr>
<tr>
<td>Cory-thornless</td>
<td>Rubus parviflorus</td>
</tr>
<tr>
<td>Mommoth</td>
<td>Rubus occidentalis</td>
</tr>
<tr>
<td>Stewart</td>
<td>Munger</td>
</tr>
<tr>
<td>Lawton</td>
<td>Plum Farmer</td>
</tr>
<tr>
<td>Phenomenal</td>
<td></td>
</tr>
<tr>
<td>Ideal Wild</td>
<td></td>
</tr>
<tr>
<td>Wild training</td>
<td></td>
</tr>
<tr>
<td>Evergreen</td>
<td></td>
</tr>
</tbody>
</table>

Rubus gymnocarpa
Rosa nutkana
Rosa rubiginosa
40.

SUMMARY

1. A brief history and the world distribution of the Yellow Rust disease of Rubus is given.

2. A review of literature concerning sexuality in other rusts closely related to the Yellow Rust of Rubus is appended as a supplement to this thesis.

3. An examination of both American and European specimens of the rust has convinced the writer that the American fungus, which has previously gone under the name Phragmidium imitans Arthur, is the same as the European Phragmidium Rubi-Idaei (DC.) Karstens, the older name.

4. Field observations, the results of greenhouse experiments, and histological studies of the pycnia, aecia, uredinia, and telia are included.

5. Among other climatic factors, the rainfall and free water on the leaf surface constitute the factor evidently most responsible for waves of aecial and uredinal infection.

6. Inoculations in the greenhouse have given (1) data for determining periods of time between inoculation and the appearance of various stages of the life cycle of the rust, (2) opportunity to study both grossly and histologically the development of these stages.

7. The morphology and development of this species correspond closely with that described previously by other workers on other species of Phragmidium.

8. Thirty-one host plants including species or horticult-
ural varieties of Rubus, and three species of native rose were tested for resistance and susceptibility to the rust.

9. The most susceptible host plants tested were in the order of their susceptibility (1) among the red raspberry varieties, Marlboro, Cuthbert, Golden Queen, Herbert, Cayuga, Ranere or St. Regis, and Antwerp, (2) among the black raspberries, Rubus leucodermis and the Cumberland, and (3) among the purple cane varieties, the Webster.

10. The Lloyd George red raspberry is merely disease tolerant, showing very slight infection.

11. Among the very resistant host plants, the following are of particular interest: the red raspberry varieties, Chief and Latham, the black raspberries, Munger and Plum Farmer, and the blackberry species, Rubus laciniatus, R. ursinus, and R. loganobaccus, and also the horticultural varieties known as Youngberry, Himalaya, and Mammoth.
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16. Zeller, S. M. The yellow rust of raspberry caused by
illus. 1927.
Jan. 1930.
PLATE VI.

Cuthbert red raspberry leaflet showing aecial pustules of *Phragmidium Rubi-Idaei* Karst. on upper surface. X 2.
Cuthbert red raspberry leaflet showing black telial masses following the lighter uredinia of Phragmidium Ruby-Idaei Karst. on under surface. X 3.
PLATE VIII.

Cuthbert red raspberry leaflets showing spotted effect produced on upper surface by uredinial infection of Phragmidium Rubi-Idaei Karst. Natural size.
Cuthbert red raspberry leaflets showing uredinial sori produced by Phragmidium Rubi-Idaei Karst. on undersurface. Natural size.
PLATE X.

Cuthbert red raspberry leaf showing aecial infection of *Phragmidium Rubi-Idaei* Karst. Natural size.
PLATE XI.

Microphotographs of vertical sections of Cuthbert red raspberry leaves infected with *Phragmidium Rubi-Idaei* Karst. X 800.

A. Section of immature aecium showing basal cells and paraphyses.

B. Section of immature uredinium showing stalk cells and urediniospore formation.
PLATE XII.

Microphotographs of vertical sections of Cuthbert red raspberry leaves infected with Phragmidium Rubi-Idaei Karst. X 350.

A. Section showing mature aecium on upper surface.
B. Section showing mature uredinium on lower surface.
Microphotographs of vertical sections of Cuthbert red raspberry leaves infected with \textit{Phragmidium Rubi-Idaei} Karst.

A. Section showing a telium and two uredinia on lower surface. X 125.

B. Section of telium with young teliospores on lower surface. X 350.
PLATE XIV.

A. Microphotograph of teliospores of Phragmidium Rubi-Idaei Karst. X 150.

PLATE XV.

Microphotograph of vertical section of Cuthbert red raspberry leaves infected with \textit{Phragmidium Rubi-Idaei} Karst.

A. Section through pycnia encircled by aecia. X 125.

B. Section of three mature pycnia showing pycniospores and uninucleate condition in the spore-producing hyphae. X 1000.
Camera lucida drawing of vertical section of a telium of *Phragmidium Rubi-Idaei* Karst. showing process of spore formation. X 500.
PLATE XVII.

Camera lucida drawings of vertical sections of uredinia of Phragmidium Rubi-Idaei Karst, on the lower surface of leaves of Cuthbert red raspberry.

A. Section of a mature uredinium. X 350.
B. Section of immature uredinium showing basal cells. X 500.
PLATE XVIII.

Camera lucida drawings of the three spore forms of *Phragmidium Rubi-Idaei* Karst.

A. Longitudinal section of young teliospore, showing two upper cells with large fused nuclei and the lower five with two small nuclei each.

B. Aeciospore. X 1000.

C. Urediniospore. X 1000.
PLATE XIX.

Camera lucida drawings of vertical sections of aecia of *Phragmidium Rubi-Idaei* Karst.

A. Immature aecium showing basal and so-called fusion cells. X 350.

B. Part of mature aecium showing method of spore formation. X 500.
PLATE XX.

Camera lucida drawings of vertical sections of pycnia of Phragmidium Rubi-Idaei Karst.

A. Section showing initial pycnial formation. X 350.
B. Section of mature pycnium. X 600.
1. SUPPLEMENT

COLLATERAL READING ON RUSTS

Literature pertaining to sexuality and life history of rusts with special reference to Phragmidium has been read because any investigator who attempts a problem in the rust fungi is keenly interested in all that is known regarding sexuality in the whole group. The endeavor to find out more about this process is naturally of vital importance in the study of the life history of any particular rush organism.

The question of sexuality has been a much discussed subject among those engaged in a study of the Uredinales. Many investigators working over a long period of years have found from time to time that the mechanism of sexuality is not the same in all types of the rusts. The recent investigations of Craigie (7-8-9), Allen, (1) Andrus, (2) and others have brought to light some very important facts that are tending to change previous viewpoints regarding sexuality of certain rust fungi.

Most of the literature regarding the function of sex in the rusts is concerned principally with what takes place in the primordium of the aecium, because it is here that the transition from the uninucleate to the binucleate condition is first observed.

For a long time the work of De Bary (1887) (11) was considered authoritative. He regarded certain stages of
2.

ascomycetes as homologous with the aecium formation in the Uredineae. He described the primordium of the aecium as consisting of a simple weft of hyphae which enlarged to form a dense mass having the appearance of pseudo-parenchyma. This mass seemed to correspond with the parithecia of certain ascomycetes. From its base rose hymenial cells which later abstricted chains of spores. His discussion evidently suggested a large female organ at the base of the aecium.

Massee in 1888, (14) working with *Uromyces poae* Rab., observed a clavate body in a ball of mycelium at the base of the future sorus and considered it as an oogonium. Close by was an anteridium-like organ which sprang from a distinct hypha. He described the oogonium as irregularly oblong, terminal on a hypha and cut off by a transverse septum. The anteridium was more or less cylindrical and filled with protoplasm, but later became empty and disappeared. He was not able to see the actual point of contact of the anteridium with the oogonium and hence could not definitely relate what took place in that which appeared to him as a fusion. The oogonium next became nodulose, and each nodule developed into a thick cylindrical basidium which produced spores in succession at the apex. Before fusion took place he found the oogonium had one definite nucleus, but after fusion he detected several. Massee considered the aecium cup as a unit resulting from a single fertilization. He compared it with the ascocarp in the Ascomycetes.
3.

Rosen (1892) (18) mentions nothing of a central organ, such as described by Massee. He worked with *Uromyces pisi* Pers. where the end cells of aecidiospore-bearing hyphae were uninucleate until a division had resulted in two nuclei in the vertical axis of the cell. The nucleus nearest the apex again divided and was cut off by a wall to form the binucleate spore. This left a uninucleate "basidium" ready to repeat the process.

Dangeard and Sappin-Trouffy (1893) (10) agreed with Rosen that each chain of spores is an independent structure. According to their interpretation the fusion of the nuclei in the teliospore constitutes fertilization. They placed little significance in the origin of the binucleate condition. They found the cells at the base of the aeciospores of *Uromyces erythronii* DC. to be binucleate during spore formation. The two nuclei in the end cells of the sporiferous filament, accordingly, came to lie side by side. Division of the two nuclei provided two for the cell that was cut off, and two remained in the end cell of the hypha. The same condition was reported in other rusts.

Poirault and Raciborski (16) came to a more or less similar conclusion. They believed that the two nuclei in the cells of the uredinial and telial stages had a distinct line of ancestry dating back to the basal cell of the aecium.

The work of Richards (1896) (17) on *Uromyces caladii*
shows a marked resemblance to that of Massee on *Uromyces poae*. He claims to have found at the base of the aeccium a large hypha which gave rise to short branches containing chains of spores. The terminal cell of each branch contained two or more nuclei. One nucleus migrated to the apex and divided. The two nuclei thus formed became separated by a wall. He believed that all parts of the aeccium including the vegetative mycelium contained binucleate cells.

Perhaps the most comprehensive cytological study of the rust fungi up to recent years can be attributed to Blackman in 1904, (3) Christman in 1905, (5) and Welsford in 1915,(19) the viewpoints taken by Blackman and Christman have been followed in most of the literature, and up to recently their conclusions were accepted as a whole. This review would not be complete without giving a brief account of their conclusions.

Blackman describes the mechanism which brings about the binucleate condition in the aeccium of *Phragmidium violaceum*. He believed that he observed a definite fertilization in the aeccium and stated that the Uredineae show an alternation of sexual and asexual generations. Fusion in the teliospore is only preliminary to a reduction division in which the sporidia (basidiospores) are produced. The sporidia germinate readily on the upper side of the leaf of the host and later the spermagonia (pycnia) develop to produce the spermatia (pycniospores). Blackman considered the spermatia to play no part
in aecial formation. He saw a massing of erect hypha beneath the epidermis to form a layer of uninucleate cells. Those just below the epidermis increased in size and by transverse walls became divided into an upper and lower cell with a single nucleus. The upper cell remained cubical and had a small nucleus, while the lower one had a large nucleus and became elongate. The upper cell, according to Blackman, was sterile and was soon evanescent, while the lower fertile cell gave rise to an aeciospore. The peculiar thing was that this terminal cell became binucleate and proceeded to cut off binucleate spore-mother cells. Blackman also noticed that the two nuclei in the fertile cell were of unequal size. This led him to believe that the smaller nuclei came from some other source. On further investigation he claims to have found instances where nuclei from the smaller sterile basal cells were actually passing into the fertile cells. From this he concluded that the early conception of the primitive, normal process of fertilization by means of the spermatia should be replaced by the concept that there is a fertilization of the female cell by the nucleus of an ordinary vegetative cell. The work of Welsford in 1915 (25) with the same species seemed to confirm Blackman's observations that fertilization was brought about by the migration of a vegetative nucleus to a fertile cell.

Christman (5) used two forms of the caeoma type of rust, *Caema mitens* S., infecting *Rubus* and also *Phragmidium*
6. **speciosum** Fr. infecting **Rosa humilis.** He describes the young primordial aecium as a layer just beneath the epidermis. Each cell possesses a single nucleus which occupies a central position in the cell. Certain of these cells elongate and become perpendicular to the epidermis. The single nucleus divides and the cell elongates into a narrow upper part which cuts off a small distal cell from the larger basal cell. This basal cell enlarges and becomes barrel-shaped. A series of vertical oblong cells each with a large nucleus and a nucleolus stand side by side. Up to this stage Christman's observations agree with those of Blackman. They disagree as to the behavior of the larger fertile cells. Christman saw two fertile cells incline toward each other and where their adjacent walls came in contact an opening formed and the two gametes were brought together. Thus there took place a union of two fertile cells to form a binucleate cell. Further division formed four nuclei. Two of them remained side by side in the distal end and two migrated to the base of the fused cell. A cell wall then cut off the distal portion to form the mother cell of the aeciospore. This cell again divided into an aeciospore and a smaller intercalary cell. The basal cell then repeated the process to form a chain of aeciospores.

Neither Blackman nor Christman gave any explanation as to the function of the spermagonia. Blackman and Frazer (4) in 1906 using another rust confirmed the observation of
Christman regarding the fusion of fertile cells as a reduced fertilization.

In an analysis of his work, Blackman concluded that the spermatium was a functionless male element. The fertile cells found in the formation of the aecium were designated as female organs which could either fuse in pairs or receive a vegetative nucleus by migration. He viewed the microforms as having a reduced or abbreviated life cycle in which the female organs had disappeared. In this case the sporophyte is initiated by an association of two vegetative nuclei.

Christman, on the other hand, saw the sporophyte generation as the product of the conjugation of two isogametes, spermatia were regarded as once functional asexual spores of the gametophyte.

The essential point is that both Blackman and Christman believed that the binucleate condition originated in the young aecium by either a migration of one nucleus into another cell, or a fusion of two cells to form a single binucleate one.

Gwynne-Vaughan (12) suggested that the Uredinales could be designated as a group of fungi in which the normal sexual process had disappeared and was replaced by forms of similar structure. The young aecium could then be regarded as a group of female organs having fertile and sterile cells. The spermatia could correspond to groups of antheridia. She
She suggested that the ancestral rusts bore groups of antheridia and groups of oogonia which had sterile trichogynes. The product of fertilization was a series of aeciospores which germinated directly to form promycelia. Again there could have been an alternation of vegetative generations in which the sporophyte bore simple teliospores inside of which septation took place.

Olive (15) could not agree with some of the ideas of Blackman. To him the fusing cells were the same size, nor was there a large female cell with a sterile tip, or an organ which he could call a trichogyne. In the caeoma forms he found that the hyphae cut off sterile cells at their tips and then proceeded to push up against the epidermal cells and degenerate. He found only one or two so-called conjugation gametes with a sterile hypha. The others showed no differentiation. He considered the sterile cells of Blackman as buffers rather than trichogynes. Olive found nuclear migrations also, but considered them simply as early stages of cell fusions. To him the function of the spermatia still remained unexplained.

Since the work of Blackman, Christman, and Olive there have been some important contributions to sexuality in the rust fungi. Notable among these is the work of Craigie. (7-8-9). His investigations have tended to place considerable doubt on the previous conceptions of certain phases of the sex mechanism in the Uredinales, especially regarding
the function of the pycniospores. He worked chiefly with Puccinia graminis and found that isolated infections with sporidia would produce pycnia without any initiation of aecia. However if nectar from one isolated pustule was transferred to another, aecia would appear and pycnia would cease to function in that particular pustule to which the transfer was made. He considered that there was a three-way possibility in which pustules of mono-sporidial origin might change from the haploid to the diploid condition. A plus sporidium (basidiospore) and a minus sporidium could settle close together on a leaf and the two pustules resulting could coalesce so that the plus and minus mycelia would come directly in contact, conjugate, and initiate the binucleate condition. Another possibility would be the transfer by insects of plus pycniospores from one isolated pustule to another which had minus pycniospores. The third possibility would be by a spontaneous method as yet unknown.

In his most recent publication in 1931 (9), Craigie discusses the results of his investigations, and admitting that his experiments have not entirely disposed of the question regarding the nature of pycniospores he has given evidence that they are functional at least in Puccinia graminis. He did find that plus pycnia produced plus pycniospores and minus pycnia produced minus pycniospores. Nectar from a plus pustule applied to a minus pustule produced aecia. If the pycniospores were destroyed by heat
he found that the nectar lost its potency. Craigie holds that the monosporidial mycelia are not of two kinds namely, male-bearing spermatia and female bearing spermatia, because if the pycnia are male conceptacles containing pycniospores, the female organ should be present. He regards the pycnia as active organs producing either plus or minus pycniospores.

Hanna (13) found sterile wefts of mycelium in the haploid pustules of *Puccinia graminis* near the lower epidermis. He found these hyphae appearing transversely, crescent-shaped and uninucleate. He considered these as possible haploid rudiments of aecial cups waiting to be stimulated into developmental activity. When the nectar of one sex is applied to the pycnia of the opposite sex, these hyphae change from the haploid to the diploid condition. An enlargement of the nuclei at the base of each weft takes place. A paired fusion of neighboring hyphae (as described by Christman) results, and chains of binucleate cells are cut off which later divides into intercalary cells and aeciospores. Hanna believes there is a possibility that a stimulation results from bringing together pycniospores of opposite sex. This stimulus produces haploid hyphae which grow down to the hyphal wefts near the lower epidermis and fuse with the cells of the opposite sex. However, these haploid hyphae have not been traced, and as he says, await further investigation.

Along with these recent noteworthy contributions are
to be mentioned the noteworthy cytological studies by Allen (1). She traces heterothallism in \textit{Puccinia graminis} and mention is made of the presence of pycnia before the sporophyte generation both in the long and short-cycled rusts. This may indicate the probability that the pycnium has a function in the short-cycled rusts similar to that in \textit{Puccinia graminis}. She sees no significance in cell fusions in the aecia of short-cycled rusts when it is considered that there are several instances where binucleate hyphae are found at an earlier stage, even before the formation of basal cells in the sorus, and even in the mycelium. According to her, the origin of the sporophytic generation is still only suggestive and the fusion of two pycniospores, or the fusion of a pycniospore with a paraphysis have not been proven. She suggests that there may be an interlacing of plus and minus mycelia and a fusing of the mycelia cells. Again two or more mycelia may anastomose and the plus and minus hyphae would then contribute to form the same pycnium. Both would form spores within the same pycnial cavity. Such a condition would be hard to prove, because, according to Allen, the hyphae look alike. It seems logical to conclude that this could bring about fertilization within the pycnium without an outside fertilizing factor.

This last suggestion has some significance to the writer in such autoecious rusts as the genus \textit{Phragmidium}. This would seem more probable when we find cases where the
pycnium still persists after it is surrounded by aecia and aeciospores.

A more recent contribution to sexuality in the rusts has been published by Andrus (2). It is of significant interest to note that he has observed what seems to be a functional sexual mechanism resembling a trichogyne which projects through the stomate or between epidermal cells of the host leaf and fuses with the spermatia. This mechanism originates from hyphae extending from the primordium of the aecia. He noted nuclei passing downward through the cross-walls of these hyphae and migrating into the fertile cells of the aecium,
13.

LITERATURE CITED


