

CONTINUOUS RUST PROPAGATION WITHOUT SEXUAL REPRODUCTION.

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With the demonstration of heterœcism in the rusts, the teliospore came to be looked upon as primarily a resting spore, for heterœcism was first proved for the black rust of grasses, in which the teliospore is a true resting spore. It was therefore believed by implication, indeed often stated, that the teliospore is the means of carrying rust fungi over unfavorable weather conditions and is especially equipped structurally for that function. The other spore forms and the mycelium, except in the comparatively rare cases of a mycelium diffused through and perennial in the tissues of the host, were not supposed to be able to survive such adverse conditions. Later when modern cytological methods were applied to the rusts, it was found, as some leading uredinologists had already suspected in a rather vague way, that the essential feature of the teliospore is that it is the structure in which is begun the series of nuclear phenomena which close the sporophytic stage and precede the gametophytic stage with its resulting sexual fusions. With this latter idea goes the rather common belief that no type of life, plant or animal, except perhaps the very lowest, can long maintain a high degree of vigor without at least occasional sexual fusions. It is this idea that has given rise to the belief held in many places that if all the barberry bushes could be destroyed, the black rust of cereals would not be able to maintain itself more than a few years. Thus we have superimposed one upon the other in the minds of many men these two ideas: (1) that the teliospore is necessary to the continued existence of the rust because it is the means of passing the winter or other unfavorable season, and (2) that it is necessary to the vigor of the fungus because it is the structure in which are initiated those changes which culminate in sexual fusions and without which such fusions would not take place. The continued prevalence early in the season of the grain rusts at great distances from any possible æcia of the species, however, led some investigators to doubt the validity of the beliefs just recorded. In consequence, a number

of investigations were made which showed, as suspected, that the rusts in question do have other means than the teliospore of surviving the winter and that in all likelihood they are able to propagate themselves indefinitely in an asexual manner, and that without serious impairment of vigor. In this paper it is proposed to give the results of this work and to present some field data, chiefly from Indiana, which was made available to the writer by his access to the Arthur herbarium. This data goes to indicate that what is true of the grain rusts is equally true of some others which because of their lack of economic importance have thus far escaped this sort of investigation.

DURATION OF VIABILITY OF UREDINIOSPORES.

Before entering on the discussion proper, however, it seems best to treat here two points which have a bearing on what is to follow; namely, the duration of the viability of urediniospores and the distance to which they may be blown and produce infection. As to the duration of germinability in the urediniospore, more work has been done with the grain rusts perhaps than with any other. In the case of *Puccinia graminis* Hungerford reports¹ finding germinable urediniospores at Madison, Wis., on timothy in October, November, December, January, and March; but it does not seem to be at all certain that the spores used on the last named date were wintered spores. On the contrary, it is altogether possible that they were but recently produced. Mercer,² however, was not able to find germinable urediniospores of the same rust on the same host during the winter in North Dakota; and Eriksson and Henning,³ as the result of several experiments with the rust on different hosts, came to the conclusion that the fungus does not pass the winter in the uredinial stage in Sweden. They also came to the same conclusion in regard to *P. glumarum*.⁴ Bolley⁵ reported the germination of 8-15% of urediniospores of *P. graminis* after twenty-one days in dry air in August. The same investigator has shown⁶ that the urediniospores of the leaf rust of wheat can be used for successful infection material after thirty days' exposure to the outside air in July, while Freeman and Johnson consider it possible for urediniospores of *P. graminis* and *P. rubigo-vera* to survive the winter in Minnesota, North

¹Phytopathology 4:337-338. 1914.

²l. c. 20-22.

³Die Getreideroste 38-47. 1896.

⁴l. c. 153-159.

⁵Centralblatt für Bakt. Par. und Infekt. 4: 893. 1898.

⁶Agricultural Science 5:263. 1891.

Dakota, and Wisconsin.⁷ Fromme has shown⁸ that the period of viability in the leaf rust of oats, *P. coronata*, may be as extended as eighty-four days. The spores in this case were stored dry in a gelatin capsule. Marshall Ward⁹ succeeded in securing germination of urediniospores of *P. dispersa* which had been for sixty-one days in dry air in the diffused light from a north window. Thus, while urediniospores are capable of germinating as soon as mature, they are capable under proper conditions of maintaining their viability for a period of two to three months and probably more. One of these conditions seems to be dryness. Probably the most common limiting factor to long life of urediniospores in nature is a combination of warmth and moisture. In such a case germination probably takes place, thus of course forestalling any long duration of life in the spore. There seems to be no good reason, however, if germination can be avoided, why urediniospores might not survive the winter. That coldness of weather does not destroy ability to germinate is attested by the fact that a number of investigators—Hungerford,¹⁰ Ward,¹¹ Carleton,¹² and others—have collected viable urediniospores of various grass rusts during the winter months.

DISTANCE WHICH WIND BLOWN SPORES TRAVEL AND PRODUCE INFECTION.

It seems to be a fact, although from the nature of the case not fully proved, that urediniospores of the rusts may travel long distances by the wind and produce infection. This, of course, is to be expected of a structure which can stand drying for so long a time and is so light in weight. Klebahn¹³ calls attention to a sand storm which arose in northern Africa and progressed northward over Europe, transporting various mineral particles to various places in Europe. He adds that without doubt the rust spores, which are much lighter than the mineral particles, are much easier transported by air currents. Under the circumstances they would remain suspended much longer and could be carried at least as far and perhaps farther than the mineral particles. The same investigator¹⁴ proved the presence of spores in the air high off the ground by constructing traps for the spores and exposing them in trees and on buildings. He was able in

⁷Bur. Plant Ind. Bull. 216:52. 1911.

⁸Bull. Torrey Club 40:518. 1913.

⁹Ann. Mycol. 1:138. 1903.

¹⁰Phytopathology 4:337-338. 1914.

¹¹Ann. Myc. 1:132. 1903.

¹²Div. Veg. Phys. and Path. Bull. 16:44. 1899.

¹³Die wirtswechselnden Rostpilze 68. 1904.

¹⁴l. c. 68.

this way to capture a large number of spores, many of which were urediniospores of the rusts. It is clear, therefore, that urediniospores may be carried many miles in the air; and there is apparently no reason for thinking that they may not then start infection. Doubtless they do start infection and in this way produce a number of isolated areas of rusted plants.

As for epidemics, however, there is evidence that they are not caused by spores brought from a great distance. One item of this evidence is furnished by Pritchard,¹⁵ who was unable to capture any urediniospores of *P. graminis* at Fargo, North Dakota, in a series of trials extending over a period of nearly a month, until the rust was common on wheat in the neighborhood. Pritchard's trap was a dish set on a five-foot post and containing a little water. Another item is the fact that in the spring, as described by Christman,¹⁶ the earliest outbreak of leaf rust on wheat is a rather heavy one on the old, wintered leaves. The old leaves then die and a period of approximately four weeks follows in which little or no rust can be found, followed by another free infection. If the epidemic were initiated by spores blown from far away, we would not expect a heavy infection early in the spring. Instead we should expect a very light early infection increasing gradually to the full epidemic later on. Further evidence of the limited distance to which spores blow in anything like sufficient quantity to produce an epidemic is found in recorded observations where it was possible to know the source of the spores producing the infection. Perhaps the species which are most limited in this respect so far as observations recorded up to the present time go are *Uromyces andropogonis*, *Puccinia andropogonis*, and *P. ellisiana*, all of which, according to observations made by Long¹⁷ are limited to an area within six feet distant from the aecia. These observations are in harmony with our own general experience in collecting rusts near Lafayette and elsewhere. The aeciospores cause free infection to a distance from their source depending upon the height of the source from the ground, but the distance is almost always small. As to the distance to which aeciospores of *P. graminis* blow in considerable quantity there are published observations by Arthur,¹⁸ Pritchard,¹⁹ Mercer,²⁰

¹⁵Bot. Gaz. 52:183. 1911.

¹⁶Trans. Wis. Acad. Sci. 15:106. 1905.

¹⁷Jour. Agr. Res. 2:303-304. 1914. Phytopathology 5:170. 1912.

¹⁸The aecidium as a device to restore vigor to the fungus. Proc. 23rd meeting Soc. Prom. Agr. Sci. p. 3. 1903.

¹⁹Bot. Gaz. 52:178. 1911.

²⁰Phytopathology 4:22. 1914.

and others. The greatest of these values is that reported by Pritchard, whose statement is here quoted: "The rust was abundant within 25 yards of the barberry bushes, but practically disappeared at a distance of 60 yards. The most persistent searching was required to discover a single pustule beyond 80 yards." Another observation by Pritchard²¹ indicated that urediniospores of *P. graminis* are carried only short distances in sufficient number to cause an epidemic. We have the published record, however, of rust spores having been blown as much as a mile and producing infection; and, strange as it may seem, the spores in question are the smallest, most delicate ones in the life cycle of the rusts if we omit the non-functional pycniospores, namely, the basidiospores. E. T. Bartholomew²² gives a table which shows that 59.1% of the leaves on apple trees near cedars were infected with rust. A quarter of a mile away it was 55.4% and a mile away it was 6.5%. All this does not show, of course, that rust spores are not carried by the wind for long distances in a vigorous condition, but it does show that the distance for abundant infection from any spore producing center is not great.

With this as a basis it should be possible to obtain an idea of the maximum distance a rust might be expected to progress in a season. The greatest distance recorded above is one mile, but those spores would doubtless travel a mile and a half farther (or two and a half miles) and produce infection. As a factor of safety, let us double this value; and as a further factor of safety, let us double this latter value. This gives us ten miles. A rust generation, according to Freeman and Johnson,²³ takes eight to twelve days, and more in cold, bad weather; and our own results at the Purdue Experiment Station agree very well with those figures. Assuming, then, ten days for a rust generation, ten miles of migration per generation, a growing season from the middle of April to the middle of October, approximately 180 days, and good weather with no interruption to the growth of the fungus, we should expect it to migrate for a distance of 180 miles. This value will be used presently in comparing the telial distribution of some of the rusts with their possible aecial distribution.

PROPAGATION OF INDIVIDUAL SPECIES.

The black rust of grasses was among the first to be observed living, and apparently thriving, at long distances from any of its aecia. There

²¹Bot. Gaz. 52:184 1911.

²²Phytopathology 2:255-6. 1912.

²³Bur. Plant Ind. Bull. 216:45. 1911.

seems now not to be the least doubt but that it can pass the winter in the uredinial stage; in fact, McAlpine²⁴ claims that in Australia the æcia of the rust do not exist and that the rust will not infect the barberry. As to the exact method of wintering there is some difference of opinion. The contention by Pritchard²⁵ that teliospores or mycelium in the seed grain have something to do with its propagation in wheat is different from all the others in the suggestiveness that a sexual process may be involved even in the absence of the æcium. All other theories which have been advanced assume a strictly asexual propagation, and probably Pritchard's theory does not really assume otherwise either. Perhaps the most famous theory is Henning's now discredited mycoplasm theory. The real means by which the rust passes the winter is probably mycelium in the leaves of the host plant. The presence of this mycelium during the winter months has been shown by Hungerford²⁶ and by Johnson²⁷ in the leaves of timothy.

That the leaf rust of wheat is carried through the winter in the same way is shown by the findings of Bolley,²⁸ Carleton,²⁹ and Christman.⁶⁰ This method of carrying the fungus over accounts satisfactorily for the heavy early infection, followed by a period of little or no infection, which is in turn followed by the epidemic proper. The old leaves, which are infected from the autumn, carry the first epidemic and then die, the mycelium, of course, dying with them. In the meantime the new leaves have been infected; and in about four weeks, which as has been shown by Freeman and Johnson,³¹ and by Christman,³² is the approximate incubation period for that time of year, the uredinial stage breaks out freely on them.

Aside from the work with the grain rusts, not much has been done in the way of determining the method of passing the winter by rusts in regions remote from their æcia. Carleton,³³ however, states that *Puccinia montanensis* on *Elymus* winters in the uredinial stage, and calls attention to the situation with regard to the bluegrass rust. This rust, *Puccinia Pourum*, is found over most of North America. Only in the far west, however, does it produce teliospores, and so only in this region can it have

²⁴Rusts of Australia 66-67. 1906.

²⁵Bot. Gaz. 52:169-192. 1911. Phytopathology 1:150-154. 1911.

²⁶Phytopathology 4:337-338. 1914.

²⁷Bur. Plant Industry Bull. 224:12-13. 1911.

²⁸Microscopical Journal Mch., 1890: 59-60.

²⁹Div. Veg. Phys. and Path. Bull. 16:21. 1899.

³⁰Trans. Wis. Acad. Sci. 15:98-107. 1905.

³¹Bur. Plant Ind. Bull. 216:56. 1911.

³²Trans. Wis. Acad. Sci. 15:106-107. 1905.

³³Bur. Plant Ind. Bull. 63:20. 1904.

æcia. It is so common throughout central and eastern regions early in the season, as well as later, that the idea of any seasonal migration from its region of possible æcia is clearly absurd. It must pass the winter in the uredinial stage, and it probably does so as mycelium in the leaves of the host. We have here a case of a rust which certainly maintains itself in a fair state of vigor for some years without the intervention of æcia and probably maintains itself indefinitely. Of course it is possible that it is constantly being renewed in vigor in the west by the presence of the æcia, and that the fungus thus renewed in vigor is slowly but continuously migrating eastward; but such a hypothesis strikes one as being fanciful rather than likely to be true.

Puccinia Sorghi, the corn rust, is another species with a wide distribution. It is usually not difficult to collect in any field of corn after tasseling time. The infection is usually not heavy, however. The æcia occur on *Oxalis*, but they occur so seldom that they seem to have little to do with the actual propagation of the rust. It is probably carried over from one year to the next by urediniospores which survive the winter or by the uredinial stage in living plants in southern regions. The latter source of infection seems more likely for this rust than for wheat rust because of its later appearance and less severity.

Puccinia Asperifolii, the leaf rust of rye, is a rust which has no known æcia in this country. Its case in America is therefore comparable with that of the bluegrass rust in this region or of *P. graminis* in Australia. It has to maintain itself by the sporophytic stage only.

Uromyces caryophyllinus on carnation is another rust which has no æcia in this country. There is no direct evidence that it can maintain itself over winter, for it usually appears in greenhouses; but it must have passed through thousands of uredinial generations since it was introduced, yet it seems to show no particular loss of vigor.

Puccinia Chrysanthemi is a Japanese species which has been introduced into America and Europe. It attacks cultivated chrysanthemums, chiefly in greenhouses. It has now been known in this country for about a decade and a half, and during this time it has never, so far as is known, produced a teliospore, although in northern Japan and in the mountains of Japan they are common. During this time no great impairment of vigor seems to have taken place, although chrysanthemum growers are able to keep it in check by the use of resistant varieties and by the exercise of care in watering.

The rusts so far considered are some of the more ordinary species, belonging to the Aecidiaceæ. There are species in both the Uredinaceæ and the Coleosporiaceæ, however, which seem to have the same ability to maintain themselves indefinitely in the uredinial stage.

Among the Uredinaceæ two of the most common rusts are *Melampsora Medusæ* on *Populus* and *M. Bigelowii* on *Salix*, both of which have æcia on *Larix*. The æcia are so much alike that it is impossible with our present knowledge to tell them apart. It seems well here, therefore, to consider the two species together, although there are definite morphological characters in the urediniospores which mark them as clearly distinct from each other. The collections of *M. Bigelowii* in the Arthur herbarium show its presence in nine counties of the State, the first collection being made in 1887 and the last one in 1914, both in Tippecanoe County. The rust is common and the epidemic is usually severe. The only explanation which seems reasonable for not having collections from all counties in the State is in the lack of collectors being at work in those not represented. *M. Medusæ* is represented by collections from five counties in Indiana, and the same remarks as to prevalence and severity that were applied to *M. Bigelowii* apply to this species also. Both of these rusts have a range also far to the southward and westward of this region. Their æcia, to the present time, have not been collected nearer this region than New York and Wisconsin. However, it is likely that they do occur nearer because the larch has a range extending as far south as northern Illinois and northern Pennsylvania. It also occurs occasionally as an ornamental tree at various places in the State. The æcia probably occur within the hundred eighty mile distance from the northern half of the State and perhaps from all parts of the State. It does not seem reasonable to think, however, that æcia occur within several hundred miles of the southern range of the fungi. The natural assumption is, therefore, that they are able to pass the winter in the uredinial stage.

Bubakia Crotonis, on *Croton monanthogynus*, has been taken four times in Indiana, from at least three counties, and over a period of time extending from 1896 to 1912. It also extends as far north and west as Nebraska. No æcium is known for the rust, but the nature of the fungus suggests a Pinaceous host and a cœmoid æcium. *Cœoma strobilinum* on *Pinus palustris* and *Pinus taeda* has been suggested by Arthur.⁵¹ Neither of

⁵¹Bull. Torrey Club 33:519. 1906.

these species of pine, according to Sudworth,³³ has a range extending farther north than the southern border of Tennessee. This distribution is well outside the 180 mile limit established earlier in this paper. Two other species of pine, *P. chinata* and *P. virginiana*, have a distribution which might possibly meet the requirements, but there seems to be no evidence other than their distribution that they carry the æcia of this rust. Since *Cronton monanthogynus* is an annual, the evidence seems to favor the idea that the urediniospores are able to survive the winter.

Two species of *Pucciniastrum* occur in Indiana, *P. Agrimonia*, on *Agrimonia*, and *P. Hydrangea*, on *Hydrangea*. The former has been taken in five counties in the State at various times since 1896, and usually the infection is severe. *P. Hydrangea* has been taken three times in Tippecanoe county only. No æcia are known as yet for either of these species, but the æcia of the different species of *Pucciniastrum*, so far as known, are species of *Peridermium* on leaves of *Abies* and *Tsuga*. Judging by the distribution for these trees given by the manuals, Indiana is probably just outside of a 180-mile zone south of their distribution. These trees are often planted for ornament, however, and the possibility exists that the æcia are to be found in the State. The rust occurs, however, as far south and west as the state of Mexico in the country of Mexico, and it is not to be expected that a species can travel so far in a season.

Among the Coleosporiaceæ, there are at least four species which have been collected in the State under conditions which lend color to the idea that they were carried over the winter in the uredinial generation. The rusts of the genus, *Coleosporium*, have their uredinia and telia on various broad leaved plants. Their æcia are leaf inhabiting species of *Peridermium* on pines. *Coleosporium Terebinthinacea* was collected in the autumn of 1912 and 1914 on *Silphium terebinthinaceum* in a restricted area near Lafayette. In the latter season, the species was limited to a patch a few rods in extent; other *Silphium* plants in the same patch were unaffected; and no affected *Silphium* plants could be found across a small ravine, although unaffected ones occurred in abundance. Other plants a mile or so away in two directions were examined but were found uninfected. The æcial stage of this rust is not known, and so it is impossible to say positively how near to this locality the æcia may approach. The nearest collection of *Peridermium* on pine leaves to be found in the Arthur herbarium is an undetermined collection on *Pinus virginiana* from Mammoth

³³Forest Atlas. Geographic distribution of North American Pines. Part I, Maps 25 and 35. 1913.

Cave, Ky. Mammoth Cave, as well as can be told by scaling on the map, is approximately 215 miles from Lafayette. It is conceivable, of course, that a wind-borne spore from such a *Peridermium* could have started the infection of *Silphium* plants each year; but when we consider the likelihood that the two species do not belong together, and the fact that the rust was found in practically the same place both times, together with the fact that the host is a perennial plant, it seems more reasonable to think that the original infection was started by a stray spore, and that its further propagation and carrying over the winters was accomplished in the uredinia! stage, either by surviving spores, or by mycelium in the living host.

A somewhat similar case is that of *Coleosporium Ipomoeæ*, which has been collected repeatedly in Tippecanoe County since 1895 on *Ipomoea pandurata*. It occurs in great abundance and is doubtless to be found in practically all parts of the State where this host is found. The same thing is true for this species as for the preceding regarding the alternate stage and the possibility of the epidemics being started by æciospores, with this addition, that because of the more general distribution and greater commonness of the fungus, it is much less likely to be started each year by æciospores.

Coleosporium Vernoniae, on different species of *Vernonia*, has for its aecial stage *Peridermium carneum* on *Pinus Elliottii* and *P. palustris*. It has a very wide distribution in the State, being represented in the Arthur herbarium from eight counties. The hosts of the æcia according to Sudworth³⁶ and Small³⁷ are both confined to an area south and east of central North Carolina and the north third of Alabama. This distance from Lafayette, as scaled on the map, is approximately 430 miles, a distance about 2.5 times as large as our maximum distance which we might expect a rust to migrate in a season. Moreover, it has been collected at Lafayette in different years as early as July 18 and July 24, which dates are early enough in the season to render it even more unlikely that the infections were developed, even indirectly, from æciospores of the same season.

Coleosporium Campanulæ is a species occurring in Indiana on *Campanula americana*. The æcium is known as *Peridermium Rostrupi* and occurs on *Pinus rigida* in eastern Ohio. The closest approach of the range of the host to Lafayette, according to Sudworth's map³⁸ is in eastern Ohio, which is

³⁶l. c. Map 35.

³⁷Flora of the Southeastern United States 33. 1913.

³⁸Forest Atlas. Geographic distribution of North American Pines. Part 1. Map 26. 1913.

approximately 250 miles distant. That the fungus at least sometimes winters over is evidenced by the fact that it has been collected in the vicinity of Lafayette on rosettes of the host as early in the season as May 6. There is little or no doubt that it had wintered in the unredinial stage, probably as mycelium in the living leaves of the host.

Perhaps the clearest indication of the survival of the winter by urediniospores or mycelium outside of the Aecidiaceæ occurs in *Colcosporium Solidaginis*, on *Solidago*, *Aster*, and a few other Carduaceous hosts. This species is very widespread throughout the United States and is exceedingly common. Its exceeding commonness is attested by the fact that its Indiana distribution is represented in the Arthur herbarium by 44 mounted collections and a few unmounted ones, from 10 counties, and extending over a period of time from 1890 to the present. The aecial stage, *Peridermium acicolum*, occurs on *Pinus pungens* and *P. rigida*, with a distribution from Massachusetts and central New York to central North Carolina. According to Sudworth's maps³⁰ *Pinus rigida* is the one of these two aecial hosts which is nearer this section. Its nearest approach, as already shown, is eastern Ohio, which is approximately 250 miles distant from Lafayette. This is a greater distance than we would expect the fungus to migrate in one growing season; but the fungus extends also much farther to the west and northwest, so far, in fact, that it seems almost absurd to think it could have spread so far from its aecial base in a season. Furthermore, the writer on the first and second of July in 1912 made collections in eastern Indiana which show that the species was already well established for the season in a region a mile or more in extent. For such an infection, spores must be present in some quantity or must be present very early. But this is not the most convincing evidence at hand. There is a collection from Lafayette on *Solidago ulmifolia*, made June 25, 1896, and one on *S. scrotina* made May 15, 1901. There is also one on *Aster cordifolius* made May 30, 1896, and one on *Aster* sp. indet. made May 12, 1902. This last collection is on the rosette leaves of the plant which were practically in contact with the ground, and the rust is well developed. The collection was actually made earlier in the season than any aecial collection of the rust at hand except one, which was made at Durham, N. C., May 3, 1910. The range for the aecial collections is May 3 to July 6; and it was clearly impossible for this specimen to have resulted from infection tracing back to aeciospores of the same spring. The circumstance seems to be much more easily ex-

³⁰I. c. Maps 26, 30.

plainable by assuming that some urediniospores or mycelium survived the winter.

It seems fair, then, to judge from the foregoing that a good many rusts can pass the winter and propagate themselves for a long time, and probably indefinitely, without the intervention of sexual reproduction. This is in line with the experience of Freeman and Johnson,⁴⁰ who carried *Puccinia graminis*, *P. rubigo-vera*, and *P. simplex* through 52 uredinial generations without apparent degeneration, and of Fromme,⁴¹ who similarly carried *P. coronifera* on oats through thirty-seven uredinial generations, and of carnation raisers generally, who still find the carnation rust an enemy to be fought although it has in all probability never produced an æcium on this continent.

The evidence, therefore, which is to be gained from the behavior of the rusts concerning the question as to whether or not a plant species can long maintain a high degree of vigor without sexual reproduction is quite definitely in favor of the idea that it can. True it is that in the long cycled rusts an effect of stimulation follows the stage in which the sexual fusions take place, but this effect becomes dispelled by one or two uredinial generations, so that the rust is then back at the old level of vigor: and it remains there through an indefinite number of uredinial generations.

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⁴⁰Bur. Plant Ind. Bull. 216:34. 1911.

⁴¹Bull. Torrey Club 40:510-511. 1913.