A GENERAL REVIEW OF THE PRINCIPAL RESULTS OF SWEDISH RESEARCH INTO GRAIN RUST.[1]

PROFESSOR DR. JAKOB ERIKSSON.

SINCE 1890 extensive researches into grain rust have been carried on at the Experiment Station of the Royal Swedish College of Agriculture. The results of these researches from the years 1890 to 1893 will be found in an extended official report,[2] and from the years 1894 to 1896 in a series of smaller papers in different journals.[3] The general review of the principal results of these investigations, which I am about to give, can best be set forth in some general theses that comprehend the sum of the results obtained.

[1] Lecture before the second Scandinavian Congress of Agriculture at Stockholm, July 20, 1897.

[2] J. ERIKSSON and E. HENNING.—Die Getreideroste, ihre Geschichte und Natur. so wie Massregeln gegen dieselben. Stockholm: P. A. Norstedt & Sön, 1896, 8vo (2; VII+463+1).

[3] J. ERIKSSON, Über die Specialisierung des Parasitismus bei den Getreiderostpilzen (Ber. d. deutsch. bot. Ges., 1894, 292–331); Über die Förderung der Pilzsporenkeimung durch Kälte (Centralbl. f. Bakter. u. Paras.-Kunde, 1895, Abt. 2, 557–565); Ist die verschiedene Widerstandsfähigkeit der Weizensorten gegen Rost konstant oder nicht? (Zeitschr. f. Pfl.-Krankh., 1895, 198–200); Welche Grasarten können die Berberitze mit Rost anstecken? (*Ib.*, 1896, 193–197); Welche Rostarten zerstören die australischen Weizenernten? (*Ib.*, 1896, 141–144); Neue Untersuchungen über die Specialisierung, Verbreitung und Herkunft des Schwarzrostes (Jahrb. f. wiss. Bot., 1896, 377–394); Studien über den Hexenbesenrost der Berberitze (Puccinia Arrhenateri Kleb.) (Cohn's Beitr. z. Biol. d. Pfl., 1897, 1–16); Vie latente et plasmatique de certaines Urédinées (Compt. rend., 1897, 475–477); Der heutige Stand der Getreiderostfrage (Ber. d. Deutsch. Bot. Ges., 1897, 183–194); Einige Bemerkungen über das Mycelium des Hexenbesenrostpilzes der Berberitze (*Ib.*, 1897, 228–231); Zur Charakteristik des Weizenbraunrostes (Centralbl. f. Bakt. u. Paras.-Kunde, 1897, Abt. 2, 245–251); Neue Beobachtungen über die Natur und das Vorkommen des Kronenrostes (*Ib.*, 291–308); Schutzmassregeln gegen die Berberitze (Zeitsch. f. Pfl.-Krankh., 1897, 65); Über den Berberitzenstrauch als Träger und Verbreiter von Getreiderost (Die landw. Vers.-Stat., 1897, 83–95) und Weitere Beobachtungen über die Specialisierung des Getreideschwarzrostes (Zeitsch. f. Pfl.-Krankh., 1897, 198–202).

1. *The kinds of fungus which produce rust in cereals are at least ten in number (partly species, partly specialized forms of species), and the spread of the disease from one kind of cereal or grass to another is thereby considerably restricted.*

In order to illustrate the situation of the grain rusts in this regard, I would call attention to the accompanying table, in which can be seen what the former situation was, that is to say, in 1890 when this investigation began, and what it is now in the summer of 1897.

At the first glance this table shows how different the position is now from what it was formerly. Then we supposed that three species of rust were found on our cereals; one of them called *Puccinia graminis* occurred on all the four cereals, another *P. rubigo-vera* (*P. straminis*) on rye and wheat, and a third *P. coronata* on oats, to which finally a fourth form, *P. simplex* on barley, was added, ordinarily considered to be only a variety of *P. rubigo-vera.* We also thought that all the kinds of Gramineæ that bore a certain species of rust (*P. graminis* is observed on a hundred species of Gramineæ in Sweden) were able to infect one another.

How different our apprehension must now be! It appears that if we stop with the four cereals we have to count in Sweden not less than ten different forms of rust, and I have cause to suspect that on the continent of Europe one or two other forms are to be found. These ten forms are distributed among at least five species in such a way that there occurs

(1) One form of black rust on rye and barley,
(2) One form of black rust on oats,
(3) One form of black rust on wheat,
(4) One form of yellow rust on wheat,
(5) One form of yellow rust on barley,
(6) One form of yellow rust on rye,
(7) One form of brown rust on rye,
(8) One form of brown rust on wheat,
(9) One form of dwarf rust on barley, and
(10) One form of crown rust on oats.

SYSTEMATIC TABLE OF THE FORMS OF THE GRAIN RUST FUNGUS, PUCCINIA.

Formerly: (1880): Species Variety.	1 GRAMINIS Pers. (Aecidium Berberidis)		2 RUBIGO-VERA DC. (Aec. asperifolii)		SIMPLEX Kcke.	3 CORONATA Corda (Aec. Rhamni)		
Now (1897): Species:	1 GRAMINIS Pers.[4] Black rust (Aec. Berberidis)	2 PHLEI-PRATENSIS Er. & Hen. Timothy rust (Aec. –)	3 GLUMARUM (Schw) Er. & Hen. Yellow rust (Aec. –)	4 DISPERSA Er. & Hen. Brown rust (Aec. Anchusae)	5 SIMPLEX (Kcke.) Er. & Hen. Dwarf rust (Aec. –)	6 CORONIFERA Kleb. Crown rust (Aec. catharticae)	7 CORONATA (Corda) Kleb. (Aec. Frangulae)	8
Specialized forms:	1 SECALIS on *Secale cereale* " *Hordeum vulgare* " " *jubatum* " *Triticum repens* " " *caninum* " " *desertorum* " *Elymus arenarius* " *Bromus secalinus* 2 AVENAE on *Avena sativa* " " *elatior* " " *sterilis* " *Dactylis glomerata* " *Alopecurus pratensis* " *Milium effusum* " *Lamarckia aurea* " *Trisetum distichophyllum* 3 TRITICI on *Triticum vulgare* 4 AIRAE on *Aira caespitosa* 5 AGROSTIDIS on *Agrostis canina* " " *stolonifera* " " *vulgaris* 6 POAE on *Poa compressa* " " *caesia*	on *Phleum pratense* " *Festuca elatior*	1 TRITICI on *Triticum vulgare* 2 SECALIS on *Secale cereale* 3 HORDEI on *Hordeum vulgare* 4 ELYMI on *Elymus arenarius* 5 AGROPYRI on *Triticum repens*	1 SECALIS on *Secale cereale* 2 TRITICI on *Triticum vulgare* 3 AGROPYRI on *Triticum repens* 4 BROMI on *Bromus arvensis* " *Bromus brizaeformis*	on *Hordeum vulgare*	1 AVENAE on *Avena sativa* 2 ALOPECURI on *Alopecurus pratensis* " *Alopecurus nigricans* 3 FESTUCAE on *Festuca elatior* 4 LOLII on *Lolium perenne* 5 GLYCERIAE on *Glyceria aquatica* 6 HOLCI on *Holcus lanatus* " *Holcus mollis*	1 CALAMAGROSTIS on *Calamagrostis arundinacea* " *Calamagrostis lanceolata* 2 PHALARIDIS on *Phalaris arundinacea* 3 AGROSTIS on *Agrostis vulgaris* " *Agrostis stolonifera* 4 AGROPYRI on *Triticum repens* 5 HOLCI on *Holcus lanatus* " *Holcus mollis*	1 EPIGAEI on *Calamagrostis epigeios* 2 MELICÆ on *Melica nutans*

Between certain of these forms, that is to say, those which constitute a species (for instance the three forms of black rust) we have not succeeded in discovering, even with the aid of a microscope, any distinguishing difference in the outer appearance, such as the size, color, and distribution of the pustules, the shape and size of the spores, etc. However, there is a difference between them with regard to their inner nature that is of no little practical interest. The difference appears in that every form is almost exclusively confined to its particular cereal, and that consequently it is able to infect no cereal but that one. Thus stems of oats bearing black rust can propagate black rust to oats, but not to rye, wheat, or barley; stems of rye bearing crown rust can propagate crown rust to rye, but not to wheat, and so on. Plants of rye and barley attacked by black rust make an exception to this rule, as they are able to infect one another; in some cases also those of wheat propagate black rust to other cereals.

If we consider the thirty-seven kinds of grasses mentioned in the table, we observe that the forms of rust upon them distinguished at the present time reach the number of thirty, and that these forms are brought together under seven species.

The old *P. graminis* has been divided into two species, that is to say, *P. graminis* (black rust) with æcidium, and *P. Phlei-pratensis* (timothy rust) without æcidium; *P. rubigo-vera*, its form *simplex* included, has been divided into three species, *P. glumarum* (yellow rust), *P. dispersa* (brown rust), and *P. simplex* (dwarf rust); and finally *P. coronata* into two species, *P. coronifera* (crown rust) with æcidium on *Rhamnus cathartica*, and *P. coronata* with æcidium on *R. Frangula*. Two forms, the last two in the table, are for the present arranged separately because we have

[4] In this column are yet to be arranged the forms of black rust on the following nine grasses: *Aira flexuosa*, *Alopecurus nigricans*, *Elymus glaucifolius*, *Panicum miliaceum*, *Phleum Boehmeri*, *P. Michelii*, *Poa chaixii*, *P. pratensis*, and *Triticum unicum*, with regard to their capacity for passing to a barberry. So far it has not been possible, on account of lack of æcidiospores, to range each of these forms in its proper place in the species.

not yet been able to effect any tests by which their true place can be defined.

We can easily see that the consequence of this abundance of forms ought to be a very considerable reduction in the capacity of the rust to propagate itself from one species of grass to another. To be sure rye and barley are able to infect one another with black rust, as illustrated in the table, and they also can be infected by *Triticum repens*, *T. caninum*, and several other grasses. In the same manner oats may be infected with black rust from *Dactylis glomerata*, *Alopecurus pratensis*, and several other grasses. For all the other eight forms of rust occurring on our cereals, however, as well as for the forms of rust on the wild grasses and the fodder grasses generally, it has not been possible to discover any source of the disease among surrounding grasses of other species.

But some one may ask if the proofs brought forward for the difference between the forms—proofs which have been gathered from experiments with the fungi in their uredo stage, as they occur on culms and leaves of grasses—are completely satisfactory. If it is a fact, as seems to follow from the table, that all forms of black rust are like each other in that they are able to alternate on barberry, producing an æcidium upon it, of course the query presents itself whether this bush is not able to serve as a connecting bridge between the forms which show their distinguishing features in the uredo stage; whether, indeed, an æcidium that, for instance, arises from the black rust on oats may not be able to produce an outbreak of black rust not only on oats, but also on the other cereals, nay, on every grass that is susceptible to black rust. Many trials made during the last six years have proved conclusively, however, that it is not so. An æcidium arising from black rust on oats is able to infect, among the cereals, only oats, while an æcidium arising from black rust on rye or barley can produce rust only on rye or barley, and so on. The different forms of black rust are thus entirely separated one from another in all their stages—as uredo and puccinia on the grasses and as æcidium on barberry

—and the small propagation of black rust by external infection, mentioned above, is not at all affected by the intervention of the barberry.

2. *The propagation of rust is often slight* (a) *between species of Gramineæ capable of bearing the same specialized form,* (b) *to and from the æcidium host* (*where there is one*), *and sometimes* (c) *between different cultivated varieties of the same cereal.*

By reference to the table we observe that the form of black rust first mentioned, called *f. sp. secalis*, may occur on rye and barley, as well as on *Triticum repens*, and several other grasses. In middle and southern Sweden *T. repens* is more often and abundantly attacked by black rust than any other grass. It would be natural to suppose that if the several Gramineæ named grew in the vicinity of one another and one should be attacked the infection would ordinarly spread to the others. If so, rye and barley ought to be frequently attacked by black rust. Such, however, is not the case. Barley is comparatively little affected by this form of rust, and rye does not suffer from it to any great degree.

It has been observed, furthermore, that barley growing near *Triticum repens* covered with black rust has remained clean week after week, although the weather had been very favorable for the propagation of the disease. We may incidentally allude to other observations in which the propagation of the disease from rusted stalks to the æcidium host, or contrarily from this plant to susceptible Gramineæ has been much less than we expected.

But, also, propagation of rust has very often appeared to be small between different cultivated forms of the same kind of cereal, and even between different individuals of the same grass. There is, indeed, scarcely an agriculturist who has not sometimes observed that different varieties of wheat are very differently attacked by yellow rust. One variety may be almost clean, while another is entirely destroyed. Such a case which was particularly noted may be here related. In the summer of 1894 a variety of winter wheat (Horsford's pearl wheat), very susceptible to yellow rust, was cultivated at the Experiment Station in a small plat. Round this plat five other varieties of wheat were sown, also in small plats, all these varieties being well known for several years as very little susceptible to yellow rust. On May 11 the middle plat showed traces of yellow rust. After thirty-three days the rust had increased a little, and after ten days more the rust had reached its maximum, the greatest degree of destruction. But at the same time all the surrounding plats at the end of the thirty-three days were clean, and at the end of the following ten days two plats still continued quite clean, and the other three only showed small traces of rust. All the plats were sown on the same day, and the weather during the last part of May and the beginning of June was part of the time very rainy.

Here we have an example of what is usually called the different susceptibility of varieties to disease. Such a different predisposition for yellow rust we have up to this time been able to point out with certainty in different varieties of wheat and barley. In view of observations made during the summer of 1896, I have reason also to suspect such a predisposition in the different varieties of wheat for brown rust, a kind of rust, however, that has but subordinate practical interest in Sweden.

Sometimes we find only a slight propagation of rust, even between different individuals of the same wild grass. I have observed specimens of *Festuca elatior* badly attacked by *Puccinia coronifera* alternating with healthy ones, or specimens of *Poa pratensis* destroyed by *P. Poarum* alternating with healthy ones, or specimens of *Brachypodium silvaticum* attacked by *P. Baryi* among completely healthy ones.

3. *The germinating power of the uredo- and æcidiospores is often small, or at best capricious.*

The fact that the yellow rust in wheat shows so little transmission from one variety of wheat to another has led to making the germination of summer spores (uredo- and æcidiospores) the subject of special investigation. It appears that in certain kinds of rust these spores are uniformly very capricious in their germination, and even sometimes absolutely refuse to germinate, even if they lie in water for four or five days. Such is the case for instance with the uredospores of yellow rust (*Uredo glumarum*), with æcidiospores of black rust (*Æcidium Berberidis*), and so on.

The cause of this remarkable state of things has been a matter of much perplexity, and many experiments were set on foot in order to learn a way of increasing the germinating power, at least to some extent. Such a way was finally discovered, which was to cool them. Ever since the old Roman days cultivators have observed that alternating cool nights and warm days favor the development of rust. From this the thought came to me to cool the spores by putting them on ice, or by chilling them in water for several hours. How strange it is, indeed, that these experiments should often give positive results! The dormant power of germination is brought to life, and with certain kinds of spores only in this manner has it been possible to carry out infection experiments. This capricious germination partly accounts for the small propagation of the disease already mentioned. But this alone does not give complete explanation, for such a restricted propagation is also to be observed in forms whose spores as a rule germinate very well. The whole cause must, therefore, be sought elsewhere.

4. *The spread of rust depends to an important degree upon the distances.*

For the purpose of explaining the outbreak and spread of rust in grain fields we have not generally been concerned with the distances separating the fields from a suggested source of infection. The pustules of rust once appearing on the barberry, the primary source of the whole neighborhood's infection was thought to have been found. It was believed that at first the nearest fields became rusted, through them in eight days afterwards the somewhat remote region, and so on. The farther from the original source, the more secure one could be. Sometimes, however, this protective distance must apparently be considerable. Black rust has been observed in the Indian wheat fields with no barberry as the source of infection nearer than 300 miles, on the Himalayas. However, we sometimes find recorded a different opinion. Thus, one of the most respected authorities in this subject, Professor Julius Kühn, of Halle, proclaimed the opinion in an official report of 1875 that a distance of 100 meters between the barberry bush and the grain field may be considered sufficiently protective.

During the last few years many experiments have been set on foot at the Experiment Station, and many observations made in the open field, in order to gain some knowledge regarding this important question, and all these experiments and observations point to the same conclusion. They show that the matter of distance is of the greatest importance, as well in the spread of the disease in spring from rusted Gramineæ to barberry, etc., as in a like spread in summer from barberry, etc., to the Gramineæ, and finally from one of the Gramineæ to another. This has been found true not only for a single year, but for all the years, at least five, that I have had my attention turned to the subject. By observation on the rust's appearance upon *Triticum repens* at different distances from a barberry bush it has been proved beyond doubt that the influence of the bush does not extend farther than 10 to 25 meters.

For these reasons it was insisted upon in the circular, which a short time since was sent out to several of the officials in Sweden, that no barberry, wild or cultivated, be permitted to grow at a distance less than 25 to 50 meters from a grain field.

5. *The germinating power of the winter spores* (*teleutospores*) *depends upon certain external conditions, and is restricted to a short period of time.*

The winter spores of black rust are capable of germination in spring only in case they have been exposed to quite natural conditions of cold, snow and rain, during the previous winter; and consequently rusted litter preserved in a barn or in a stack is not to be regarded as dangerous. This has been fully demonstrated in the results of the first four years as given in the detailed report.

Observations and experiments made during the current year have brought to light still another matter of interest concerning the germinating power of the spores. It appears that only the crop of spores maturing during late autumn is able to germinate the following spring.[5]

All that I have now set forth — (1) the multiplicity of fungous forms producing the rust disease, (2) the obstinacy of some uredo- and æcidiospores in germination, (3) the great importance of the matter of distance, and (4) the conditional and short-lived germinating power of the teleutospores — cannot well be brought into agreement with the view which has been held, and is yet generally prevalent, with regard to the outbreak and propagation of grain rust, and we may perhaps say of parasitic plant diseases in general, viz., that it is the continual accession of new infective material and the continual formation of new centers of infection which cause the outbreak and the intensity of the disease. The five theses set forth above give each in its degree a hard wrench to the corner stone upon which the whole doctrine of grain rust has been resting for a long time.

It may be asked whether this overthrow of prevailing opinions is the only or principal result of the investigations. Does it not present some more positive result, some new starting-point upon which a new doctrine may be founded, and from which new work may begin? I am obliged to be brief at this time, and to give merely a short and summary review of my results, referring for details to the special works already published or soon to be published.

I shall first call attention to two observations that were easily made, but no less remarkable for that reason. Each of them gave cause to suspect a source of rust quite different from that which we have been accustomed to look for.

6. *The yellow rust appears in certain varieties of wheat and barley that are especially susceptible, uniformly four to five weeks after sowing.*

7. *The intensity has sometimes been stronger in sunny than in shady places in the same wheat field.*

These two observations, together with the results from sev-

[5] Details will soon be published elsewhere.

eral special investigations upon the succession of the rust pustules, etc., related in the work "Die Getreideroste," could not fail to excite suspicion that perhaps the source of disease is an internal one, included within the plant itself.

How then test whether this suspicion might be right or not? The first experiments made with this in view showed that

8. *Wheat plants, which early in the spring, immediately after the melting of the snow, were enclosed in long and large glass tubes stuffed with cotton wool above and below, and consequently carefully protected against external infection, developed stalks that after six to eight weeks showed yellow rust.*

There is no possibility of explaining this outbreak of rust through external infection taking place immediately before or after enclosing in the tubes. The immediate sources of the disease in these cases must have been an internal one. Here two possibilities seem to suggest themselves. The first is that in late autumn of the previous year, during early growth of the wheat, an external infection came from teleutospores or uredospores of the yellow rust, germinating upon the seedlings; and that the fungus afterwards lived a hidden internal life until the full outbreak in the spring. The other possibility is that germs of disease had been inherited by the seed grain from the parent plant itself.

In order to decide between these two possibilities it has been necessary to arrange the experiments in a special way. Therefore I have sowed grain in sterilized soil and protected the growing plants from external infections by raising them in glass houses constructed so that the air could pass in only through cotton-wool filters. Such experiments in glass houses of different construction have been carried on for four years, and have shown that

9. *Plants of a variety of barley extremely susceptible to yellow rust, grown in sterilized soil and protected from external infection in isolated glass houses, have sometimes become rusted.*

These results prove beyond doubt that the disease must come from internal germs inherited from the parent plant.

But in what form are these internal germs of disease living? Is it easy to follow and identify them with the microscope? Not at all. They can only be detected just before the breaking out of the young pustules. The microscope examination induces me to suppose that

10. *The fungus lives for a long time a latent symbiotic life as a mycoplasma in the cells of the embryo and of the resulting plant, and that only a short time before the eruption of the pustules, when outer conditions are favorable, it develops into a visible state, assuming the form of a mycelium.*

To speak comprehensively, the investigation above outlined gives the following general conclusions:

A. The outbreak of grain rust is due (a) *in the first place to germs of disease in the host plant itself, which in certain cases are inherited from the parent plant through the seed, and in which they lead a latent symbiotic life as a mycoplasma and continue to do so afterwards for a long time in the resulting plant, and* (b) *in the second place to external infection from the vicinity.*

B. The intensity of grain rust is due (a) *in the first place to the degree with which the dominant outer circumstances* (*weather, soil, manuring, and so forth*) *are able to convert the inner germs of disease from the latent stage of a mycoplasma into a visible stage of mycelium, and* (b) *in the second place to the accession of infective material from without.*

So far have we now gone in our knowledge of the nature of grain rust. Many things that before seemed incomprehensible have now a natural explanation, and our point of view has been very much changed. Especially have the experiments so far carried out provided a new method for explaining the varying susceptibility of different varieties of cereals, and have thus given a new point of departure for continued efforts for the mastery of the disease in the open field. We are warranted in suggesting that the predisposition of the Hosford wheat to yellow rust may be explained by assuming that between this variety of wheat and the yellow rust an extremely vital mycoplasma-symbiosis is to be found, while on the contrary the Squarehead wheat is nearly exempt from the rust for the reason that no such symbiosis has arisen between this wheat and the fungus.

With this fundamental view as a point of departure we have yet to ascertain to what degree we can by different manures, by different treatment of the soil, by different time of sowing, etc., influence the internal germs of disease in such a manner that the transformation from the latent mycoplasma stage to the sporiferous mycelium stage may be as much as possible delayed and prevented. We have further to make use of the knowledge gained in the selection and cultivation of varieties as little susceptible to the disease as possible. We have to find out to what degree by crossing we can combine a small susceptibility to rust with a strong resistance to cold, and finally whether certain regions may not tend to repress the development of the inner germ of the disease, and thus become regions for the production of certain kinds of cereals.

The questions above mentioned are of great practical importance, and they suggest a very rich field for further investigations

STOCKHOLM, SWEDEN.