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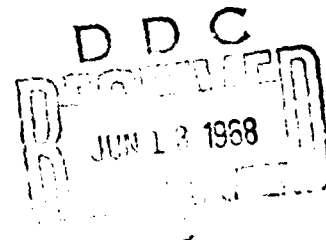
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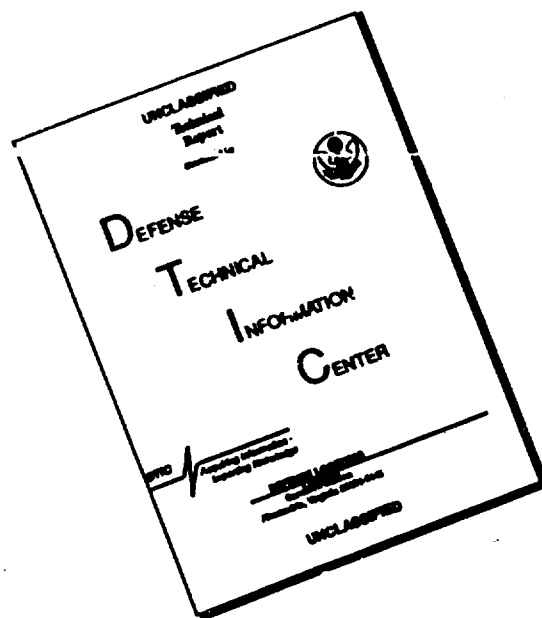
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**THE GRAIN RUSTS: THEIR HISTORY AND NATURE
AND MEASURES TO BE USED AGAINST THEM**

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THE GRAIN RUSTS: THEIR HISTORY AND NATURE,
AND MEASURES TO BE USED AGAINST THEM

Meddelanden från Kongl. Landbruks-Akademiens Experimentalfält
Reports from the Experimental Field Prof. Dr. Jakob Eriksson
of the Royal Agricultural Academy) Dr. Ernst Henning
Vol. 38, 1910, pages 210-259

4. Puccinia dispersa Eriks. & Henn., nov. spec. -- Brown rust.
Plates X-XI, Figures 119-123 [Not reproduced here].

Diagnosis: I. Aecidium Anchusae. -- Aecidia circular or elongated, yellow-red, more or less swollen spots, formed by preference on the leaf (blade as well as petiole) and stalk, but also on the calyx and seed-bud. Spores prickly, 20-30 μ in diameter or 20-30 x 19-22 μ .

II. Uredo dispersa. -- Clumps (pustules) 1-1.5 mm long and barely 1 mm wide, strewn irregularly over the whole surface of the leaf without forming continuous fields, brown (brown ochre, "sienna"). Spores spherical to slightly elliptical, prickly, yellow, 19-20 μ in diameter.

III. Puccinia dispersa. -- Groups of spores, covered by the epidermis, forming more or less continuous irregular black borders on the under side, rarely on the upper side of the leaf blade. Each group of spores divided into numerous compartments, each compartment surrounded by a border of brown paraphyses which enclose it in a ring. Spores short-stemmed, for the most part long and claviform, asymmetrical. The length of the spores 40-50 μ , width of the basal cells 12-15 μ , that of the terminal cells 14-19 μ . Spores germinating as early as autumn. Sporocyst developing on the promycelium colorless.

Exsiccatae: I [see Note]. Eriksson, Fung. par. scand. 18 (Anchusa arvensis, Skåne, 16 August 1881). -- Syd., Ured. 631 (A. arvensis, Germany, 22 August 1891). -- Von Thümen, Herb. myc. oec. 267 (A. arvensis, Germany, June 1874); 452 (A. officinalis, Denmark, August 1876); Myc. univ. 230 (A. Arvensis).

Germany, summer of 1874).

[Note] Only those aecidia forms are included here which occur on Anchusa arvensis and A. officinalis, and which are the only ones that can be asserted with more or less probability to belong here.

II and III. Syd., Ured. 121 (II, III, Bromus mollis, Germany, June 1889; 7628 (II, B. mollis, Germany, June 1892); 7629 (II, B. sterilis, also on sheaths, Germany, June 1892); 7630 (II, B. tectorum, also on sheaths, Germany, June 1892). -- von Thüm., Herb. myc. 71 (II, Triticum vulgare, Bohemia, June 1872); 72 (II, III, Secale cereale, Bohemia, June, 1872); Fung. austr. 784 (II, Secale cereale, Austria, July 1871); 785 (II, III, Bromus mollis, Austria, June, 1871) [see Note].

[Note] In the recently published fascicle 9 of Eriksson, Fung. par. Scand., the following forms of this species appear: 417, f.sp. Secalis (II, Secale cereale, Exp., 14 July 1894); 418, f.sp. Triticici (i, Triticum vulgare, Exp., 13 July 1894); 419, f.sp. Agropyri (Exp., Triticum repens, II, 11 September 1894); III, 18 September 1894); 420, f.sp. Bromi (II, Bromus arvensis, Exp., 5 October 1894); 421 (II, B. brizaeformis, Berg., 10 October 1894); 422 (II, B. secalinus, Exp., 13 July 1887); 423 (II, B. arduennensis, Berg., 27 August 1891); 424 (III, B. racemosus, Exp., 15 July 1885). [The same number contains 14 numbers (402-415) of Puccinia graminis, 1 number (416) of P. Phlei-pratensis, and 6 numbers (425-430) of P. glumarum.] --Late note, 18 September 1895.

Host Plants: I. Anchusa arvensis (Sk.--Exp.). -- A. officinalis (Sk.--Upl., Osteråker, 5 August 1892: B.J. Hesselman).

II and III. Bromus arduennensis (Berg., II, 27 August 1891). -- B. arvensis (Exp.). -- B. patulus (Berg., II, 23 October 1891). -- B. squarrosus (Berg., II, 6 September 1892). -- Secale cereale (Smål. [see Note], Lyckås-Upl., Wattholma). -- S. montanum (Berg., II, 23 October 1891). -- Trisetum flavescens (Berg., II, 27 August 1891; 6 September 1892). -- Triticum compactum (Exp.). -- T. dicoccum (Exp.). -- T. Spelta (Exp.). -- T. vulgare (Exp.).

[Note] In the rye and wheat plots of the experimental field of the agricultural institute at Copenhagen this species was found in the greatest abundance in the early days of July 1892, so that there is every reason to assume that it must also occur in Skåne.

Historical. -- If we wish to get from the descriptions in the available literature a reliable knowledge of whether in each case the brown rust (Puccinia dispersa) which is to be discussed here or the yellow rust (P. glumarum) discussed earlier or perhaps a third closely related species is the subject of the description in question, we do not arrive at complete certainty in most cases. For it will usually be found that the description in question partly fits one and partly the other of the two species mentioned above, and this is quite particularly the case when we take account not only of what is said about the uredo stage but also of what is said about the puccinia stage. The difficulty of

forming a firm conviction in the question before us from the information contained in the literature is also substantially increased by the fact that it is not yet known whether the species of brown rust isolated here behaves in exactly the same way when it appears in southern countries as it does in this country, and specifically whether it restricts itself there, too, to the leaf blade of the cereal species attacked, or whether in milder climates it can also occur on other parts of the host plant.

There are only a few cases in which we can identify our species of brown rust confidently from the descriptions. We encounter the first case in Ørsted, who in 1863 describes (I,100) and illustrates (Plate 3, Figures 2a, 3) a form occurring on the blade of the rye leaf that has "somewhat larger and more oval clumps than the wheat rust" (= Puccinia glumarum) "scattered all over the blade of the leaf" and possesses spores that are "almost oval or spherical." There is no doubt that Ørsted is concerned here with Uredo dispersa itself, even though he assumes that it is a form of "grass rust" (Puccinia graminis) which in attaching itself to the rye leaf has changed the shape of its spores while retaining its color. This supposition of Ørsted's led Nielsen (II,375) in 1874 to undertake infection experiments with the oval-spored form occurring on wheat stems and sheaths, and when these experiments produced no round-spored, brown uredo form on the rye leaves he had inoculated, the next year (IV,499,518) he attributed the round-spored form to "wheat rust," with the explanation that this latter species "forms rounder, scattered spots of somewhat darker color when it occurs on the leaves of rye, rye grass, etc." No special infection experiments carried out with the round-spored form are mentioned [see Note].

[Note] Bolley's representation of the species Puccinia "rubigo-vera" in North America is especially noteworthy. If we were to draw any conclusions from the circumstance that in 1890 (III,6) he includes, as he had done earlier, the uredo forms of both Puccinia graminis and P. "rubigo-vera" under the name "red rust," we might be inclined to conjecture that the American Puccinia "rubigo-vera" was really the P. dispersa described here, if not a species coinciding with it in color. But the same investigator asserted the year before (II,7) that the wheat in Indiana was attacked by three species of rust, which he called Puccinia graminis, P. coronata, and P. "rubigo-vera." of which the "last two are subepidermal" and the last (II,12) "the most destructive." The conjecture suggests itself that by Puccinia coronata Bolley may have meant our P. glumarum, but hardly P. dispersa. If this conjecture should be confirmed, Puccinia dispersa might turn out to be the most important but not the only form of P. "rubigo-vera" in North America.

We may also be sure that it must have been Puccinia dispersa, in the puccinia stage, that de Bary (V,209) had before him in 1865 when he performed his successful experiments of

infecting Anchusa arvensis (and A. officinalis) with teleuto-spores, -- the first and at the same time the only infection experiments that have been carried out to our knowledge with teleutospores of Puccinia "rubigo-vera" on boraginaceae.

a. The Rest Stage of the Fungus During the Winter

1. Uredo Dispersa on Cereal Seeds. -- Like those described earlier, this uredo form can, at least in certain years, occur on the seedlings of winter sowings even before the beginning of winter, although its intensity both at this time and later in the spring and summer, at least in the vicinity of Stockholm, is less than that of the closely related yellow rust. In the late autumn of 1891, in the examination of the winter sowing field on 23 and 24 October, Uredo dispersa was found on only two rye plots out of twelve examined, while at the same time Uredo glumarum was found on all (97) wheat plots and about half the rye plots. It is not impossible, however, that if the examination of the plots, which at that time was primarily aimed at the economically far more important yellow rust, had been carried out with greater exactness than was actually the case, several other plots besides the two rye plots mentioned above would have been counted among the brown rust victims.

In the late autumn of 1892 Uredo dispersa was very numerous on a large number of plots of both rye and wheat. At the time of the first examination on 6 October, 36 days after the sowing, on the larger experimental field traces of it were found on three rye plots out of a total of thirteen examined and on 27(-34) of 91 wheat plots examined. On the next examination day, 17 October, 47 days after the sowing, it was found on five rye and 42(-49) wheat plots, and on the last examination day, 7 November, 68 days after the sowing, on three rye and 53 wheat plots, the number of plots examined being the same on both days as on the first day.

During the same autumn the observations were made somewhat more often on a smaller experimental field which was especially arranged for observation of the rust forms on winter wheat and which contained 14 experimental plots sown with 13 different varieties of winter wheat. On this field spots of brown rust were found

on 26 September, 24 days after the sowing, on	0	% of the plots			
" 1 October, 29	"	"	"	"	25 % " " "
" 6 October, 35	"	"	"	"	42.8 % " " "
" 17 October, 46	"	"	"	"	42.8 % " " "
" 7 November, 67	"	"	"	"	57.1 % " " "

It is the most obvious assumption that these uredo colonies on the seedlings originated through infection by uredospores from the neighboring rust-infected summer plots,

since infected summer plots were present in great abundance and the uredospores of this species of rust generally show a good germinating power. But if we assume this mode of origin it is difficult to explain satisfactorily the long delay in the outbreak of the spots. If in the case of the smaller of the two experimental fields we deduct the not more than ten days that elapsed from the time of sowing until germination, we see that the time during which the leaves were exposed before the spots appeared on them was

19 days in	25	% of the cases
25 " "	17.8%	" " "
57 " "	14.3%	" " "

This time is surprisingly long when we compare it with the approximately 10-day incubation period that we found in artificial infection experiments with this uredo form indoors. This long delay in appearance of the spots in the field, on the assumption that the sole origin of the spots is to be sought in a uredo infection, compels us to assume further that the cotyledons had been attacked by the infecting uredospores not immediately after budding out, but only much later. Such absence of infection in the first weeks appears not a little strange, however, for we must assume that the supply of infectious material at that very time is incomparably richer and the prospect of a successful contagion much greater than later. We can therefore hardly avoid considering the question whether the source of the spots is not in greater or less part other than that assumed above.

Another conceivable explanation would be that the spots were due to an Aecidium Asperifolii nearby. The probability of such an origin is practically nil, however, since that aecidium was not present either in the experimental field or in the vicinity, although boraginacea such as Nonnea, Anchusa, and Symphytum were by no means lacking there.

A third mode of origin of the above uredo is also conceivable, namely infection from germinating teleutospores. Grounds for this supposition could of course be found in the circumstance that such spores occurred in great numbers on leaf remnants left lying on the field from the wheat harvested shortly before, and that these spores are capable of germinating throughout the autumn and late autumn, or in other words at the time when the winter grain is sown and germinates. On the other hand, as in the case of the species of rust described previously, decisive proof of the existence of such direct spore infection of the seedlings is lacking.

There is also a lack of evidence to explain these uredo spots -- as a fourth possible mode of origin -- on the basis of a contagious material hidden inside the seed grain.

Satisfactory explanation of the occurrence of this uredo

form on the seedlings of winter grain becomes much more difficult in places where there is not such a multiplicity of varieties of grain ripening at different times as there is in the experimental field described above. Such a case came to our notice when we found Uredo dispersa as well as Uredo glumarum on rye seedlings that were sent to us from Ekeby, near Södertelje, 7 November 1892. In answer to our inquiry the sender, Mr. J. Lundvall, stated that neither he nor his neighbors grew summer rye or summer wheat, that the nearest summer wheat field was about 1 1/3 kilometers away from the affected rye field and separated from it by a projecting tip of woodland, and that while Anchusa arvensis could be found at a distance of about 2000 feet from the field, it had no detectable trace of rust on it and was not found in the affected field or neighboring fields. These reports did not justify us in attributing this species of rust either to a grain cultivated in the vicinity, which might have been able to bear the fungus in this uredo form in the late autumn, or to an Acididium Asperifolii occurring in the neighborhood. This leaves only the assumption that the disease either was caused by contagion from the uridineae of wild grasses, e.g. Bromus, -- an assumption, however, which is not very probable, since, as will be shown later on, there appears to be a strict specialization of the parasite in this species of fungus as there is in others [see Note], -- or by germinating teleutospores, which can be assumed to be present in the leaf remnants of some neighboring field already harvested, or, lastly, that it had its origin in a disease germ hidden inside the seed grain. The extent to which it is justifiable to favor one or more of these possible explanations must remain undecided.

[Note] According to the new investigations of 1894 (Eriksson, V, 315) the form on the Bromus species does not appear capable of infecting cereal species. --Late note, 18 September 1895.

In order to learn how and at what rate this uredo form spreads on the cotyledon once attacked by it, on 7 October 1892 we had five wheat plants with rust on the first cotyledons dug up from the field and transplanted in pots. The position of the colonies was observed and described on the day of transplanting and also on 8 October, 9 October, 10 October, 11 October, 13 October, 15 October, and 20 October, or in other words daily for the first five days and then every other day and finally after three days. The results of this study of one of the leaves observed for 13 days may be seen from Figure 53 [not reproduced here], the observations of the first 3 days, however, 8-10 October, being combined and shown in the same color (red), while the next five days are shown in a different color (green) and the last five days with a third color (black). The yellow color shows the position of the original colonies on the first day. The temperature during this time showed a daytime maximum of +4.5° to 14.5° and a low at night of +1.0° to +9.0°, except for the last three nights, which were nights of freezing weather with lows of -2° to -7°.

If we study the data for these five leaves we see that the original rust spots on the first day, 7 October, were present in the following number:

3	on leaf number	1
2	" "	" 2
6	" "	" 3
5	" "	" 4
3	" "	" 5
Total		19.

Of these original rust spots only one proved so weak that its mycelium could not generate new colonies. The cases were also rare (only two) in which the colony-generating capacity of the mycelium ceased on 10 October, i.e. three days after observation of the first colony. In five cases this capacity lasted for eight days, and in eleven cases until the end of the period of observation, or thirteen days. In seven of these last eleven cases, however, the colonies came into existence slowly, so that in coloring the illustrations either red or green or both were unneeded. Especially in these seven cases the possibility that the colonies appearing later came from a new and separate infection is very great. For it is quite conceivable that in the cases where such a long time as nine days elapses before a new colony is added to one that already exists, the new one when it does appear is the result of a new contagion, or in other words that its mycelium possesses no real genetic relationship with that of the old colony beside it.

If we turn to the original data on which the summary given above is based we find that after the reading on 17 October, the day after which the temperature of the nights began to fall below the freezing point, a new colony appeared at only one place. It therefore appears that in this case cold exerted a considerable inhibiting influence on the capacity of the mycelium to form new colonies. From the time when the last precise observation was done on 20 October we have only notes of 28 October, when all five leaves were either more or less withered or so thickly infected with Uredo glumarum and U. dispersa both that an exact reading was no longer possible.

Of the new, independent colonies that appeared after the first day of observation a relatively large number were not accompanied by later colonies in their immediate vicinity. This was true in 13 cases out of 27 on the five leaves. It might be concluded from this that the later a colony appears on the autumn seedling the weaker the capacity of the mycelium to generate new colonies and the earlier that capacity comes to an end, whether an end for good and all, the common death of the mycelium and the leaf, or only a winter sleep that will yield in the spring to a new period of vitality. But among the remaining 14 cases there are 9 sure and 2 less sure in which the mycelium continued for 10 days to develop colonies.

Table 36. *Uredo dispersa* on Wheat Seedlings in Late Autumn 1892

Leaf No.	No. of Colonies of Rust								Percentage of Leaf Surface with Rust Colonies in Comparison to the Entire Surface of Leaves			
	7 Oct.		10 October		15 October		20 October		7 Oct.	10 Oct.	15 Oct.	20 Oct.
	(Yellow)	New (Red)	Total	New (Green)	Total	New (Black)	Total					
1	6	4	10	8	18	13	31	3	5	10	16	
2	3	4	7	5	12	1	13	1	3	4	5	
3	19	18	37	15	52	36	88	6	12	17	28	
4	9	32	41	33	74	43	117	2	10	18	28	
5	3	15	18	10	28	4	32	0.6	4	5	6	

How much the number of colonies on all five leaves grew during the period of observation and how great a part of the leaf surface was covered in each case is shown in Table 36. In computing the part of the surface covered by colonies the size of each colony was estimated to one square millimeter, and as a rule decimal fractions were omitted.

It will be seen from the table that the part of the surface of a leaf that the fungus gradually took up during the thirteen-day period of observation varied widely, quite independent of the apparent original energy of the fungus, but that that part in no single case significantly exceeded one quarter of the total surface of the leaf.

From what has been said it will be seen that this species of rust even in the state in which it appears on the seedlings in the late autumn shows definite characteristics in the manner of its occurrence and of its spread that differ from those encountered in similar cases with the uredo forms of black rust and of yellow rust. By its widely separated colonies and the relatively insignificant growth of each colony *Uredo dispersa* reminds us of *U. graminis*, but its growth reminds us of *U. glumarum* to the extent that it finally takes up a relatively great part of the surface of the leaf, although this goal is not reached by the direct extension of a single, originally connected colony field, as in the case of the yellow rust uredo, but by the development of a large number of new, small, independent colonies (Figure 53). In the one case, with *Uredo glumarum*, the cause of the finally great expansion of the fungus, almost embracing the entire surface of the leaf, is to be sought essentially in an inherently great developmental energy of the mycelium, but in the second, with *Uredo dispersa*, primarily in a great readiness of the uredospores to germinate and their tendency to generate new centers of the disease. Apart from these differences between the two forms the differing coloration is to be observed that is characteristic of them, the color of *Uredo dispersa* (Figure 109) being yellow ochre when it appears on seedlings -- chiefly reminiscent of

U. graminis (Figure 1), which is brown ochre in color -- while light ochre is the basic color of U. glumarum (Figure 55). This color difference of the three forms shows up best when by good fortune the three are found on the same leaf [see Note].

[Note] Sometimes on seed leaves colonies of such indefinite yellow-brown color are encountered that it is only by microscopic examination of the spores that it is possible to decide whether they belong to Uredo graminis or to U. dispersa.

2. Hibernating Uredo. -- If we consider the question of the significance that this uredo on the seedlings of late autumn may have in the developmental history and in particular in the hibernation cycle of the fungus, the answer, as appears from the observational data presented in Table 37 below, is that this significance is slight. No influence on the early date of appearance of the colonies in the following spring or on the intensive occurrence of the fungus at that time can be discovered. Although there were still colonies on all the rye plants listed in the table on 28-29 December 1891, the next spring on 2 April new uredo colonies could be found in only one case (no.1). It was not until about a month later, on 30

Table 37. Uredo dispersa in the Winter of 1891-92 in the Experimental Garden

Obs. No.	Host Plant		Trans-planted 1891	Date of Observation									
	Species	State		1891				1892					
				21/10	4-5/11	14/11	28-9/11	2/4	4/4	30/4	9/5	13/5	31/5
1	Secale cereale	Seedling	17/9	1	1	.	1 ^a	1 ^b	.	1	0	.	0
2	"	"	"	1	1	.	1 ^a	0	.	1 ^b	0	.	0
3	"	"	"	1	1	.	1 ^a	0	.	0	0	.	0
4	"	"	"	0	1	.	1 ^a	0	.	0	0	.	0
5	"	"	30/9	0	1	.	1 ^c	0	.	0	0	0	0
6	"	"	.	1	1	.	1 ^b	0	.	1 ^b	1	.	1
7	"	"	5/10	1	1	.	1 ^b	.	0	0	.	.	0
8	Bromus secalinus	Lawn	sown 25/5	1	1	1	1	1 ^a	.	0	0	.	0

Notes: a) Leaves with colonies withering. b) Leaves with colonies green. c) Colonies on both green and wilting leaves.

April, that colonies were found in two other cases (no.2 and no.6). The other four were still clean on 31 May. At that time two of the cases that had had colonies in April (no. 1 and no. 2) were also clean. But this again affords no grounds for inferences as to why the new colonies in the spring could not be derived from the colonies visible in December. Of the seven cases that had rust toward the end of December, two

(no. 6 and no. 7) bore the rust colonies on green leaves, but four (no. 1 to 4) on wilting leaves and one (no. 5) both on green and on wilting leaves. It would be reasonable to think that the spring uredo would have to appear first on the numbers that already had colonies on green leaves in December, but such was not the case. The case number (no. 1) that was first noted as rusty in the spring had borne its colonies on half-wilted leaf in December, and in two of the numbers (no. 5 and no. 6) whose colonies were on green leaves in December there was still no spring uredo on 31 May. In no single case was it possible to derive the spring uredo colonies, all of which were on fresh, green leaves, from the mycelium of the autumn uredo.

b. The First Generation of the Fungus: the Promycelium Stage

1. The Time of Germination of the Teleutospores. --

Because of the successful germination and infection experiments carried out by de Bary (V,208) in the spring of 1865 with hibernating teleutospores of Puccinia "straminis," which is synonymous with P. dispersa here, as may be concluded both from the description given by him of the progress of the germination ("colorless promycelium") and from the positive infection results on species of Anchusa,-- because of these experiments de Bary (V,213) reached the conclusion that the teleutospores of this species, like those of Puccinia graminis, "do not germinate until after hibernation." He did note that in the case of Aecidium Asperifolii "throughout the part of the year that is not cold, from spring until late fall, and in fact even in January, all developmental stages can be found." In order to account to some extent for this phenomenon -- a phenomenon whose explanation "at the time was no more possible" than "that of the annual or perennial nature of other plants" -- de Bary resorted to the hypothesis that the teleutospores which live through the winter germinate only gradually because of the thick coverings of the spore colonies, which "gradually weather away in the course of the summer," those uncovered first germinating in the spring and the others later in the year.

This view of de Bary's is found in the works of nearly all investigators since. Only Nielsen (VI,47) in 1877 and Plowright (VI,168) in 1889 expressed doubts about it. The former conjectures that these spores germinate in the same autumn in which they are formed, since Aecidium Asperifolii usually occurs on the Boraginaceae which grow among the rye stubble, and since the teleutospores were visible as early as the beginning of June on the underside of the leaves; and he has a good ground for his conjecture in the circumstance that he had actually observed a germination in the teleutospores of a closely related species of grass rust, Puccinia Poarum, in the autumn. Plowright hit upon a similar conjecture in the autumn of 1885. He had laid a sheaf of rusty wheatstraw in his garden in August in order to have usable material for his experi-

ments the next spring. To his surprise he found that a nearby Anchusa that had never been rusty in earlier years bore fully developed acedia in September of that year.

In the investigations done during the last few years at the experimental field to find out the time and conditions of teleutospore germination of this species it has been found that here, at least in material taken from rye, germination, as will be seen from Table 38, may take place immediately after the complete development of the spores, and that if the spores are kept in a protected place (barn, room) it may continue until late in the following year.

Table 38. Germinating Capacity of Puccinia dispersa from Rye

Exp. No.	Spore Crop	Material taken at the implantation stage from	Where it had been kept since	Date of Examination	Power to Germinate		
					Degree	After Days	Hours
1	1891	the room	harvesting	20 Oct. '91	germinated	3	
2	1891	" "	"	20 Oct. '91	"	2	
3	1891	experimental barn	"	31 Oct. '91	3	5	
4	1891	" "	10 October	11 Jan. '92	4	4	
5	1891	" "	10 October	13 Feb. '92	3	2	
6	1891	" "	harvesting	11 July '92	3	4	
7	1892	exp. garden (very fresh)		21 May '92	4	4	
8	1892	" - "		21 June '92	3	4	
9	1892	the field		30 July '92	1	6	
10	1892	the room	harvesting	29 Sept. '92	3	1	
11	1892	experimental barn	August 1892	19 March '93	3	2	
12	1892	laboratory	March 1893	8 May '93	3	1	20
13	1893	the field		9 Aug. '93	1	2	.
14	1893	the laboratory	7 August 1893	19 Sept. '93	3	3	

It appears as unnecessary here as in the case of the teleutospores of yellow rust to have such atmospheric influence as has been demonstrated for black rust in order to arouse the capacity to germinate. How this may be with that form of Puccinia dispersa that occurs on wheat, on the other hand, cannot be stated with certainty. Oddly enough, the germination experiments noted with these teleutospores, -- with the 1892 crop of spores on 30 July 1892 and 8 May 1893, and with the 1893 crop on 12 August, 13 August, and 16 August 1893, -- gave a negative result without exception, whether the samples were taken from the laboratory, from the experimental barn, or

directly from the field, and even though the material had lain indoors from two to six days for germination.

2. The Course of Teleutospore Germination. -- It is striking that the teleutospores of this species, although their color is not essentially different from that of the teleutospores of yellow rust, nevertheless show a very characteristic difference in their germination, in that the outthrusting germ tube, the promycelium, in this case possesses a content almost as clear as water, with very little turbidity (Figure 120), while the content of the promycelium of yellow rust is very strongly yellow in color. When it first protrudes the promycelium is relatively thick (Figure 120 a). Very soon it divides and branches, and its lowest member often grows to a considerable length without further dividing, while the outermost members segment off into sporidia which are also colorless (Figure 120 b). Sometimes, however, the promycelium remains very short, as does its base member (Figure 120 a).

3. Infection Experiments with Puccinia dispersa. -- From the description given us by de Bary (V, 208) of the course of germination in the infection experiments done in 1865 with the teleutospores of the Puccinia "straminis" occurring on Anchusa, namely that "the content both of the promycelium and of the sporidia is always colorless," we may draw the definite conclusion that de Bary in his experiments was dealing with a form of Puccinia dispersa. There was every reason therefore to expect positive results from infections with this particular species, and, as Table 39 shows, experience confirmed the correctness of such an expectation. It is at least evident that spermogonia broke out on both species of Anchusa after an incubation period of 10-15 days.

Table 39. Infection Experiments with Puccinia dispersa from Rye on Anchusa

Experiment No.	Date	Infectious Material		Infected Plants		Places of Infection		Results			
		Degree of Germinating Power	After Days	Species	No.	No.	Place	+	-	Final No. of Spots Formed	Incubation Period of Spermogonia in Days
1	29/9/'92	3	1	<u>Anchusa arvensis</u>	1	13	leaf	+		.	10
2	19/9/'93	3	3	<u>A. officinalis</u> ¹	2	11	"	+		11 ²	11-15
3	19/9/'93	3	3	<u>A. arvensis</u> ¹	1	10	"	+		9 ²	13-15

Notes: 1) The infected plants had been moved from outdoors to indoors on 12 September; control plants moved in on the same day but not infected stayed clean the whole time. -- 2) Even after 21 days no aecidia had appeared, but only spermogonia.

c. The Third Generation of the Fungus: the Aecidium Stage

1. Aecidium Anchusae. -- It is remarkable that the information that appears in the literature concerning this aecidium, which is commonly called Aecidium Asperifolii but ought rather to be called Aecidium Anchusae, since the genus Anchusa is the only genus of Boraginaceae from which or to which this rust has been artificially transferred, is scanty and as a rule would suggest a sparse population. In 1872 Nielsen (I,326) writes from Denmark, "Although the family of the Boraginaceae is hardly more abundantly represented anywhere (in Denmark) than in southwestern Zealand, by a great number of individuals of e.g. Echium vulgare, Anchusa officinalis, and A. arvensis," and "although Puccinia straminis occurs very destructively there, especially on wheat," "nevertheless, Aecidium Asperifolii is by no means abundant," and "even where Anchusa arvensis occurs one must often search long to find aecidia." The same author (V,38) says five years later that in Denmark "Aecidium Asperifolii has been observed only on Lycopsis and Anchusa, not on Echium, etc.," and that "where Lycopsis, which is relatively rare, occurred in somewhat greater numbers, rust was observed on a few plants from the beginning of June on until August," and lastly that "at this time nothing was found on Anchusa," which may have been very rusty "later, from the beginning of autumn until late autumn, especially beside rye stubble and in its vicinity."

In 1875 Kühn (II,400) reports from Germany that "the formation of aecidia may have dropped out of the cycle of Puccinia straminis, which has done the greatest damage to wheat (and rye) before its aecidium has been seen on the boraginaceae," and Voss, who in 1878 (I,83) says he has searched in Carniola often and in the most varied places on Anchusa and Lycopsis for aecidia, explains in 1889 (II,49) that such aecidia "have not been found in Carniola on those plants, and on Pulmonaria and Symphytum only sporadically — aecidia whose classification as Puccinia rubigo-vera has not yet been successfully proved." In 1882 Plowright (II,11) writes from England that "the aecidium of Puccinia rubigo-vera is very rare," and that he had "searched for it several times, but in vain," and Smith (I,181) states in 1884 that this aecidium is "so rare" there that he has "never encountered it during his thirty years' study of fungi." And in Finland this aecidium had never been seen up to 1884, according to Karsten (I,30).

It seems to be the same in other continents. From Asia Barclay (II,234) reports in 1891 that "although Puccinia rubigo-vera in India as elsewhere is the common species of rust on wheat and barley," nevertheless "no boraginaceae aecidium is known there," and that although "all the collections of boraginaceae belonging to the Royal Botanical Garden in Calcutta have been searched through, not a single suspicious leaf was to be found." From North America, Burril (I,234) reports in 1885 that "in Illinois aecidia have been seen on

no boraginaceae other than Myosotis verna," the aecidium of which, however, he explains under the name Aecidium Myosotidis as a separate form to itself, and Farlow & Seymour (I,80) in 1880 know no aecidium of any Anchusa species in North America. Finally, in Australia, according to Cobb (III,59), 1892, "no aecidium has ever been observed on Anchusa arvensis and Echium."

It is only from Denmark and very recently that a report comes to us of the abundant occurrence of this aecidium. Rostrup (VIII,65) in 1893 says that the aecidia there "sometimes occur abundantly on Lycosis and Anchusa."

As for Sweden, it seems that here too, with the possible exception of the most southerly part, this aecidium form occurs only rarely and sparsely. Only a few finds are known to us from the area around Stockholm. On a botanical excursion to the island of Lidingön on 27 July 1892 we observed some twenty individuals of Anchusa arvensis growing on a dry, sunny bank of a ditch; one plant among them had on one single leaf a beginning of spermogonia formation. During the same year at Strengnäs, inside the town itself, spermogonia were observed on a single leaf of Anchusa officinalis. In 1893 this form of rust occurred very sparsely on a few specimens of Anchusa officinalis on 12 September near Älkistan (Stockholm), and somewhat more abundantly on self-sown plants of Anchusa arvensis in the experimental garden of the experimental field, where spermogonia began to appear on 8 August. It may be somewhat otherwise in the southern parts of the kingdom, especially in Skåne, where it is by no means rare, in unharvested fields of potatoes and beets, especially the former, to see Anchusa arvensis and sometimes also A. officinalis covered with aecidia, often in great numbers. This was the case e.g. in the environs of Malmö in August of 1891 and 1892. In 1891 in the township of Kyllie, south of Malmö, aecidia were observed on 26 August on young plants of Anchusa arvensis that had been free of them a week before, and also on 19 August not far from the Ystad railway station at Malmö on older plants of A. officinalis, abundant in both cases. In the former place on the edges of a ditch nearby Bromus mollis was growing, heavily infested with Puccinia dispersa in the teleutospore stage; in the latter place no rusty grass could be seen in the vicinity, and it is also worth mentioning that the numerous specimens of Echium vulgare that were growing beside the rusty Anchusa were quite intact.

Besides the two species of Anchusa just discussed, the following boraginaceae are mentioned in the literature as bearing aecidia and are found as such in the exsiccatae: Anchusa undulata from Germany (Sydow, Ured. 374), Borago officinalis from Silesia (Schröter, III,325), Cerinthe alpina from (?) Germany (Winter, I,218), C. aspera from Italy (Erb. crittog. 896), C. minor from Hungary (Sydow, Ured. 280), Cynoglossum

officinale from (?) Germany (Winter, I, 218), C. virginicum from North America (Farlow & Seymour, I, 80), Echium vulgare from the Carpathians (Rabenhorst, Fung. europ., new edit., Series 2, 1036), Heliotropium curassavicum [Aecidium biforme Pk.; Ae. Heliotropii Tracy & Gall.] from North America (Farlow & Seymour, I, 80), Lithospermum arvense [Aecidium Lithospermi Thüm.] from Moravia (Sydow, Ured. 577), Myosotis verna [Aecidium Myosotidis Burr.] from Illinois in North America (Burril, I, 234), Nonnea pulla from Siebenbürgen (Linhart, Fung. Hung., 327), Onosmodium carolinianum from North America (Farlow & Seymour, I, 80), Pulmonaria officinalis [Aecidium Pulmonariae Thüm.] from Silesia (Schröter, III, 325) and Austria (Linhart, Fung. Hung., 1600), P. styriaca from Carniola (Voss, II, 49), Stenhammaria maritima from Jutland (Rostrup, VII, 9), Symphytum bulbosum from Italy (Saccardo, Myc. Ven., 41), S. officinale [Aecidium Symphyti Thüm.] from Silesia (Schröter, III, 325), Brandenburg (Sydow, Ured., 122), and Italy (Saccardo, Myc. Ven., 42), and S. tuberosum from Carniola (Voss, II, 49) and Bavaria (Allescher, I, 28). It remains to be found out by experiments to what extent a greater or less number of the boraginaceae listed above are or are not concerned with Puccinia dispersa.

2. The Course of Aecidiospore Formation. -- In the germination of aecidiospores, which in general takes place very readily if the spores contain the necessary amount of moisture, a thick germ tube protrudes, not branched at first, and filled with an abundant yellow content (Figure 123 a). After 24 hours the germ tubes have generally attained a length several times as great as the diameter of the spores, and they also sometimes branch out at the tip (Figure 123 b).

3. Infection Experiments with Aecidium Anchusae. -- Because of these spores' generally good capacity for germination, a relatively large number of infection experiments have been carried out with them. The material for these experiments, which are summarized in Table 40 below, was taken in 1891 and 1892 from rusty plants of Anchusa arvensis that we had had sent in from Skåne, since this aecidium is almost completely lacking in the neighborhood of Stockholm. The infection experiments of 1893, on the other hand, were done with the spore material that had been taken from the rusty specimens of the same boraginaceae which were found in that year in the experimental garden of the experimental field.

It is very remarkable that of a total of 19 infection attempts only those six showed a positive result in which the infection was done on rye, while all seven experiments done on wheat turned out negative, not to mention the experiments on barley (three) and oats (three), which were without success, just as these two cereals remained unaffected by the species of rust in question under natural conditions. In the experi-

Table 40. Infection Experiments with *Aecidium Anchusae* from *Anchusa arvensis*

Experiment No. and Date	Infectious Material		Infected Plants Species	Places of Infection		Results								
	Degree of Germinating Capacity	After Hours		No. No.	Location	7	9	11	12	13	14	16	18	22
1 26/ 8/'91	germinated	20	Secale cereale	2	2	Folds of Leaves								
2 26/ 8/'91	"	20	Hordeum vulgare	2	2	" "								
3 26/ 8/'91	"	20	Avena sativa	2	2	" "								
4 26/ 8/'91	"	20	Triticum vulgare	1	1	" "								
5 23/ 9/'91	.	.	Secale cereale	2	3	" "								3
6 23/ 9/'91	.	.	Hordeum vulgare	2	3	" "								
7 23/ 9/'91	.	.	Triticum vulgare	1	2	" "								
8 23/ 9/'91	.	.	Avena sativa	3	3	" "								
9 9/10/'91	.	.	Triticum vulgare	4	4	Tips								
10 9/10/'91	.	.	Secale cereale	3	3	" "								1
11 9/10/'91	.	.	Avena sativa	4	4	" "								
12 9/10/'91	.	.	Hordeum vulgare	3	3	" "								
13 11/10/'91	.	.	Triticum vulgare	4	4	Folds								
14 2/ 8/'92	4	12	Triticum vulgare	2	3	" "								
15 2/ 8/'92	4	12	Secale cereale	3	6	" "								6
16 29/ 8/'93	4	10	Triticum vulgare	3	12	Leaves								
17 29/ 8/'93	4	10	Secale cereale	2	14	" "								14
18 16/ 9/'93	4	7	Triticum vulgare	4	12	" "								
19 16/ 9/'93	4	7	Secale cereale	4	15	" "								

Notes: 1) The puccinia stage begun to appear 15 days after the infection. -- 2) The puccinia stage began to appear 22 days after the infection.

ments done on rye the number of positive results is no less than 38 out of a total of 41 infected. The number of infection spots made in the experiments on wheat was 38, all negative. With these results before us we cannot help but assume that the form on the rye must be a different form from that on the wheat, and that the aecidium of *Anchusa arvensis* belongs to the *Puccinia dispersa* of rye, but not to that of wheat.

In support of a similar view of the aecidium occurring on *Anchusa officinalis*, namely that it belongs to the form occurring on rye, we have the results of an infection series reported by Nielsen (V,37) in 1877. On 13 October aecidiospores from the abovementioned boraginaceae were transferred to eight wheat and twelve rye plants, all of which had been raised in pots. A new infection with new fresh spores was carried out on the same plants on the 16th to 18th of the same month. On the twenty-sixth numerous uredo colonies appeared on the rye plants on both sides of the leaf, but not a single colony on the wheat -- only pale spots. On 1 November the first two leaves of all the rye plants were thickly covered with colonies, but the wheat was still rustfree, with the white spots dying out.

As against the specialization assumed here it may be pointed out with respect to the aecidium on *Anchusa arvensis* that Flourens (VI,168) perceived the rust on *Anchusa* plants in his garden for the first time after he had some time before laid a sheaf of rusty wheatstraw in their vicinity, and with respect to the aecidium on *Anchusa officinalis* firstly what Nielsen (V,37) adds immediately after the description of the infection series just mentioned, namely that "there was better success with somewhat older wheat plants" -- though without describing in detail any specific experiments at all -- and secondly the circumstance that in one of our infection experiments described above (Table 39, no. 2) after the infection transferred from rye only spermatogonia and no aecidia appeared.

The incubation period, which according to de Bary (V, 209) runs 6-8 days and according to Nielsen does not exceed 13 days, ran in the experiments noted in Table 40 between 7 and 18 days.

d. The Third Generation of the Fungus: the Uredo Stage

1. The Time of Occurrence of the Uredo Stage and Its Varying Intensity. -- In regard to the time of first occurrence of the uredo in the spring and to the intensity that this species of rust develops in the course of the summer, investigations have shown varying results in different years, just as in the case of the species of rust discussed previously. During the first year of observation (1890) it appears, -- to judge by the relatively somewhat scanty notes of that

Table 41. Uredo and Puccinia dispersa on the Cereal Species of the Experimental Field in the Summers of 1890-1893

Summer	Date of Observation	Number of Experimental Plots														
		Winter Rye			Summer Rye			Winter Wheat			Summer Wheat					
		Clean	Rusty, by Degree		Clean	Rusty, by Degree		Clean	Rusty, by Degree		Clean	Rusty, by Degree				
			1	2		1	2		1	2		1	2			
1890	5/1	13	1		14				90			90				
	6/1	6	6		12				10	30		40				
	8/1	2	7	2	11				7	35		42				
	12/1		6	8	14				5	76	12	93				
1891	7/1	7			7				11			11				
	8/1	7			7				11			11				
	10/1	5	2		7				11			11				
	12/1	1	4	2	7					41		41				
1892	7/1	12			12				42			42				
	8/1	12			12				42			42				
	10/1	5	6	1	12				9	2		11				
	11/1	2	8	2	12				9	2		11				
	12/1		8	3	11				27	14		41				
	1/1	1	7	4	12				22	19		41				
	6/1	1	7	4	12					39	1	40				
	8/1								12			12				
1892	12/1								12			12				
	1/1								1	6		7				
	6/1								6	6		12				
	11/1								6	6		12				
	12/1								6	6		12				
	1/1								6	6		12				
	6/1								5	7		12				
1893	7/1								2	8	2	12				
	11/1	12	1		13				77			77				
	12/1	12	1		13				77			77				
	1/1	12	1		13				76	1		77				
	6/1	13			13				76	1		77	40			40
	8/1	13			13	8		8	75	1		76	40			40
	10/1	3	10		13	8		8	70	7		77	40			40
	11/1					3	5	8								
	12/1		10	3	13		8	8	33	38		71	21	1	2	24
	1/1		3	10	13		8	8	14	49	3	66	35	3	1	39
6/1							8	13	13	25	51	7	20	5	38	
8/1												4	4	6	13	

time, when no adequately sharp distinction between the forms had been made, -- that this species, as shown on Table 41, appeared in the experimental field on 31 June in at least one rye plot, and six days later on six rye and thirty wheat plots, and by the end of the month it had reached such extent and intensity in at least two rye plots that -- if we distinguish two degrees of rustiness in this species of rust, namely 1 = slightly rusty, 2 = severely rusty -- the degree of rustiness could be assessed as 2. The next year (1891) this uredo appeared in the experimental garden 4 May, but in the experimental field not until 7 July, in both cases on rye, while on the latter date nothing could be detected on the wheat of the experimental field. It was not until the beginning of August that the degree of rustiness reached 2 in two rye plots, and only then did the wheat form begin to appear in all the wheat plots.

The year 1892 appears to have been a favorable year for this species of rust. In the experimental garden it was observed on rye as early as 2 April, and in the big experimental field, where rye plots and wheat plots were interspersed, it was found on the same day, 15 June, on both rye and wheat, but obviously further developed on the rye than on the wheat, for more than half the rye plots were already infected, one of them severely, while a considerable number of the wheat plots showed only a trace of rust. Still earlier, on 4 June, it had appeared in another, smaller experimental field exclusively planted with wheat, in at least half the winter wheat plots.

The year 1893 is very peculiar. While this species of rust was found very early, on 11 April in one rye plot and on 19 May in one wheat plot, it did not really get under way until July. Despite a long standstill it finally reached such strength that this year more than any previous one, to judge by the observations made at the experimental field, may be characterized as a real brown rust year. By 29 July most of the winter rye plots were as much infested as they can be by this species of rust, and on 10 August it was the same with the winter wheat plots. On the summer rye, a grain that had not been cultivated on the experimental field in previous years, it appeared for the first time on 10 July, and exactly a month later it had seized possession of all the leaves present in all plots of this grain. Finally, it got its hold on the summer wheat somewhat later, from the middle of July until the middle of August.

2. Non-Simultaneity on Different Cereal Species. -- What has just been said is sufficient to raise the question whether there exists such a substantial lack of simultaneity of brown rust forms on the various species of grain, and on winter grains and summer grains, as we found earlier for the different forms of black rust and yellow rust. The conjecture

that such a non-simultaneity might exist was formed in the year 1891, the first year in which the relevant time observations could lay claim to any great value; in that year on 7 July two rye plots out of seven were found to be infested, while at the same time not a single spot could be found on a single one of the 41 wheat plots examined. Still, the observations of that year do not afford absolute certainty in that question, since a whole month passed from the first (24 April) to the second (25 May) observation.

In 1892 the observations are more frequent, and the question for that reason is better elucidated, at least as concerns the forms of winter wheat and winter rye in comparison with each other. The two forms show a definite time difference, both as to the first appearance and as to the real height of the season. That time difference hardly shows up if we compare the rye of experimental field I with the wheat of experimental field II; in fact the form in question is actually noted earlier in the wheat plots of the latter than in the rye plots of the former; but it shows up all the more decisively when we compare the rye and wheat plots of experimental field I with each other that were located together in the northern part of the field. The figures of Table 42 give

Table 42. Time Difference in Appearance of *Uredo dispersa* on Plots of Winter Rye and Plots of Winter Wheat in the Summer of 1892

Plots of Rye				Surrounding Plots of Wheat							
Rusty, by Degrees				Number of These Still Clean							
No.				No.	2 July		18 July		30 July		
	15 June	2 July	12 July		No.	Time Difference in Days	No.	Time Difference in Days	No.	Time Difference in Days	
1	2	2	2	5	4	27	4	31	3	45	
2	1	2	2	3	2	27	1	31	0	45	
3	1	1	2	3	3	27	3	31	2	45	
4	1	1	1	4	2	27	2	31	2	45	
5	1	1	1	5	3 ¹	27	3 ¹	31	3 ¹	45	
6	1	1	1	3	2	27	2	31	1	45	
7	1	1	1	6	4	27	4	31	3	45	
8	0	1	2	5	2	10	2	16	1	28	
9	0	1	1	3	3	10	1	16	1	28	
10	0	1	1	5	4 ¹	10	4 ¹	16	1 ¹	28	
11	0	0	1	4	2	0	2	6	2	18	
12	0	0	1	3	3	0	3	6	1	18	

Note: 1) Two of these plots were planted with the variety "Michigan Bronze," which had been almost completely destroyed by yellow rust before the brown rust appeared.

some indication of this, for on 15 June no fewer than seven plots of rye (out of twelve) were infested, one severely, while on the same day and even 14-17 days later (part of the wheat plots were examined on 29 June and the rest on 2 July) only two plots of wheat (of some forty) showed a trace of this species of rust. Not until 12 July, or almost four weeks after the first appearance of the species on rye, was its occurrence noted as a trace on a somewhat larger number of plots of wheat, and it is to be noted here particularly that of these fourteen only five were situated in the northern part of the experimental field, where plots of rye and wheat were adjacent. The other nine wheat plots were further removed from the infested rye. Even on 18 July the number of rusty plots of wheat had grown only insignificantly, from 14 to 19, and of the additional ones only two lay immediately adjacent to rusty plots of wheat.

The difference becomes still plainer when we investigate how those plots of wheat behaved that were close beside the plots of rye, either so that the plots planted with different grains touched at the sides or else at the corners. This is shown in Table 4?. If we count from the first day when the rust showed up on the rye to the first day when it was observed on the neighboring plot of wheat, we find a time difference of

45	days	in	14	cases,
31	"	"	19	"
28	"	"	3	"
27	"	"	20	"
18	"	"	3	"
16	"	"	7	"
10	"	"	9	"
6	"	"	5	"

but among these contiguous plots of rye and wheat it is noted in only five cases that the brown rust showed traces in both kinds of plots on the same day.

But a non-simultaneity also seems to show up if we compare winter grain and summer grain with each other. In the summer of 1892 this uredo form was noted for the first time

on 4 August		on 2 plots of summer wheat,
on 9 August	on another 2	" " " "
on 24 August	" " 7	" " " "
on 29 August	" " 2	" " " "

The first of these observations was made 23 days after that of 12 July, when the same species of rust had taken possession of 14 (out of 41) plots of winter wheat. In 1893 we thus find a difference of about two months in the first appearance of this species of rust on winter and summer grain and a difference of about three weeks in the height of the season. As summer rye was grown in the experimental field only the last summer (1893), the data for answering the question as to whether there is a time difference for brown rust between the

winter and summer varieties of this cereal are quite scanty in numbers. But these few data point toward a time difference of about two months in the first appearance. Once the rust had begun to show up on the summer rye, it developed such a great rapidity of spread that the difference in the greatest incidence was only slight.

3. Germinating Capacity of the Uredospores. -- As a rule the uredospores of this species show a good germinating capacity, from the beginning of spring until late in the autumn. Ordinarily the germ tube issues from only one of the germ pores, and is abundantly supplied with a yellowish-red, grainy content, somewhat darker than in the case of Uredo glumarum; it usually branches into numerous branches (Figure 115). At the tips of these branches, however, the content is colorless.

4. Infection Experiments with Uredo dispersa. -- The infection experiments done with the uredospores of this species are summarized in Table 43.

The results of these infections point in the same direction as the previously mentioned infection experiments with acidiospores of Aecidium Anchusae and the observations concerning non-simultaneity of the forms occurring on rye and wheat. These results lead us to view these forms as biologically distinct. Of all the experiments that were carried out with spore material taken from rye, not a single one of those done on wheat -- although there were six of these experiments with more than thirty infection points -- resulted in the appearance of colonies, while on the other hand the two experiments done on rye plants, with a total of only ten infection points, had a positive result in nine cases. These experiments taken together thus give well-founded cause for setting up a f.sp. Secalis as a specialized form of the species Puccinia dispersa.

On the other hand the results of the infection experiments carried out with material taken from wheat are less clear. The experiments were less numerous in this case, only three in fact, and in one experiment there were uredo colonies on rye, too, in two infection points. It is very easily possible that this result is the consequence of an impurity of the material, since in one of these experiments (no. 11) that was infected with this material colonies developed that looked very like Uredo glumarum, while in the second (no. 12) out of eight colonies two or perhaps three contained both yellow rust and brown rust (Figure 69). Since the infectious material was thus demonstrably a mixture of the two forms Uredo glumarum f.sp. Tritici and U. dispersa from wheat, we are justified in the assumption that the material might have contained U. dispersa f.sp. Secalis from the beginning as well, especially as

Table 43. Infection Experiments with Uredo Dispersa

Infections	Infectious Material		Infected Plants		Points of Infection		Results												
	No. Date	Origin	Germinating Power	Species	No.	No.	Position	No. Infected Spots After days											
			No. After Hours					8	9	10	11	12	13	14	15	16	17	18	19
1	1891 11/7	Secale cereale	4	Triticum vulgare	1	Leaves, sheaths													
2	"	"	"	Avena sativa	1	"													
3	1892 2/6	"	4	Triticum vulgare	3	Leaves Folds of leaves													
4	"	"	4	Triticum vulgare	2	"													
5	"	"	"	Secale cereale	2	"													
6	"	"	"	Triticum vulgare	2	"													
7	" 11/2	"	3	Triticum vulgare	3	Leaves													
8	1893 2/2	"	4	Triticum vulgare	4	"													
9	"	"	"	Secale cereale	1	"													
10	1892 11/7	Triticum vulgare	3	Secale cereale	2	Folds of leaves													
11	1893 11/8	"	2	Secale cereale	2	sheaths, leaves													
12	"	"	"	Triticum vulgare	3	"													

Notes: 1) There was only one point of infection, which by then was dead, on which no colonies had appeared. — 2) The infectious material used was contaminated because of the fact that there was also Uredo glumarum on infection number 12.

this form was at its height at about this time on the rye and was not farther than 30-50 meters from the experimental plot from which the experimental material was taken. Further infection experiments are needed, however, to decide whether such an assumption as the above is correct. As things now stand grounds are certainly not lacking for setting up a f.sp. Triticci within the species Puccinia dispersa as specialized. [See Note.]

[Note] Later observations concerning the specialization of this species have been reported on the basis of new experiments in 1894 (Eriksson V, 316).
--Late note, 18 September 1895.

e. The Fourth Generation of the Fungus: the Puccinia Stage

That the speed of development of this fungus is great may be concluded merely from the fact that de Bary (V, 210) in his infection experiments with aecidiospores of Anchusa arvensis started on 18 June 1865 was able to generate teleutospores early in July. Another indication of the same thing, in Nielsen's infection experiments in 1875 with Aecidium Asperifolii on rye, is the appearance of teleutospores on the twenty-third day after the inoculation (23 August).

The same thing is shown by the observations on our experimental field. The puccinia stage was observed in 1890 on rye in the field on 19 June, just six days after there had come to be reason for supposing that that plot harbored uredo, and it was observed there on wheat (17 plots) on 8 July, only eight to twelve days after uredo had been observed with some certainty on the same plots. The next year the puccinia stage was noted on rye in the field on 7 July, on the same day that the uredo had first been observed in the same plot, and in the summer of 1892 teleutospore spots appeared on the same cereal in the experimental garden on 21 May and in the field on 30 July. In the summer of 1893 we observed in two infection experiments that were carried out on rye with aecidiospores from Anchusa arvensis (Table 40, no. 17 and no. 19) that the first occurrence of the puccinia stage in one case was on the fifteenth and in the other on the twenty-second day after the infection.

f. The Cycle of Development

According to the representation just given we should have to conceive of the developmental cycle of this fungus in one or more of the ways suggested in Table 44 below. But further investigations are necessary before we can decide which of the modes of development actually occur in nature, for that there are several is obvious, since Aecidium Asperifolii, as we have just brought out, is such a sporadic phenomenon that the assumption of only a single development, the heteroecious, does not suffice to explain what at least appears to be the widespread and general occurrence of this fungus in Sweden.

Table 44. The Developmental Cycle of Puccinia dispersa on Winter Rye

Possible Origin of the First Uredo Generation of the New Year	Autumn	Winter	Spring	Summer	Autumn
I. <u>Sporidium Infection</u> on <u>Anchusa</u> and <u>Acidiospore Infection</u> on Cereal Plants ("heteroecism")	Uredo (aecidium- borne)	Resting Mycelium (aecidium- borne)	Uredo	Uredo and Puccinia	Autumn <u>Promycelium</u> and <u>Sporidium-borne</u> <u>Mycelium</u> , producing <u>Spermatonium</u> and <u>Aecidium</u> on <u>Anchusa</u> ; the <u>Aecidiospores</u> on cereal seedlings producing <u>Uredo</u>
II. <u>Sporidium Infection</u> on Seedlings (in the autumn) ("homocicism")	Uredo (sporidium- borne)	Resting Mycelium (sporidium- borne)	Uredo	Uredo and Puccinia	<u>Promycelium</u> and <u>sporidium-borne</u> <u>Mycelium</u> , producing <u>Uredo</u> on cereal seedlings
III. <u>Uredo Infection</u> on Seedlings ("hibernating Uredo")	Uredo (uredo- borne)	Resting Mycelium (uredo- borne)	Uredo	Uredo and Puccinia	<u>Uredo</u> and <u>Puccinia</u>
IV. <u>Endogenous Mycelium</u> in Seed Grain	<u>Mycelium</u> developing with the seedling from the seed, pro- ducing <u>Uredo</u> sometimes in autumn, some- times not un- til next spring	Resting Mycelium (endogenous)	Uredo	Uredo and Puccinia	<u>Uredo</u> and <u>Endogenous Mycelium</u> in the maturing seed grain

The mode of development shown last here in the table presents the greatest difficulty, since according to all we know this fungus has such a sharply defined localization that it occurs exclusively on the blade of the leaf.

g. Localization of Uredo and Puccinia dispersa

l. f.sp. Secalis. -- Sometimes in this fungus we find in the uredo stage, as soon as it appears in the spring on the lowest leaves, a ring-shaped arrangement (Figure 110). In the ring, whose greatest diameter in the lengthwise direction of the leaf may be 5 mm or even more, we see in the center one or more somewhat larger colonies, and on the circumference a great number of very small colonies. In this case the spots take up several nerve fields; this suggests that the mycelium has the tendency, when circumstances permit, -- that is when few or no continuous nerves block the way, -- to spread in rings, just as seems to be the case with several uredineae that occur on wild plants, e.g. not uncommonly with Puccinia Arenariae (Schum.) Wint. In this respect the mycelium of this species shows a distinct innate difference from that of the yellow rust, in which such a ring-shaped arrangement of the colonies is never observed. On the other hand in those leaves which possess a number of continuous nerves, or in other words in all summer leaves on the upper parts of the plants, the uredo colonies are situated where they first came out on the blade of the leaf (Figure 112 a), strewn over that surface with no definite arrangement among themselves. Even before they come out, small light spots are observable (Figure 111 a). Sometimes when the uredo appears a dense accumulation of pustules in the vicinity of the leaf fold itself is observed (Figure 111 b). In a later stage of the disease the whole upper side of the leaf may be seen thickly covered with pustules (Figure 112 b). The whole appearance gives an impression as if the leaf had been spattered by a brush dipped in brown paint, and it is this scattered location of the uredo colonies that led us to call this species dispersa.

In order to learn in greater detail the way in which this uredo form spreads on a summer leaf once attacked by it, at the beginning of July 1892 we made drawings of five leaves that had been attacked by this species of rust shortly before. Four of these rye leaves were examined three successive times, on 6 July, 12 July, and 20 July; the fifth leaf drawn was destroyed by accident. The results of these examinations are shown in Table 45.

It will be seen that during the fourteen-day period of observation the number of colonies grew considerably, and in one case even multiplied fivefold, but nevertheless the colony-bearing surface of the leaf, because of the smallness of the colonies, still did not amount in the end to more than a maximum of 25% of the whole surface.

Table 45. *Uredo dispersa* on Rye Leaves in the Summer of 1892

Leaf No.	Number of Rust Pustules					Surface Covered with Rust as % of Total Surface of Leaf		
	6 July	12 July		20 July		6 July	12 July	20 July
		New	Total	New	Total			
1	7	12	19	333	352	0.5	1.3	25.0
2	9	13	22	287	309	0.4	0.99	13.8
3	37	11	48	173	221	1.9	2.5	11.5
4	9	4	13	160	173	0.4	0.6	8.2

The teleutospore aggregates are found on the under side of those leaves which bear or have borne uredo aggregates (Figure 116 a), and are most numerous at the base of the leaf blade. They form densely placed elongated stripes (Figure 116 b) covered by the epidermis.

Theaecidia break out on the *Anchusa* species both on stems and on leaves and calyces, and sometimes even on the ovaries (Figure 121 a,b,c). The spots affected are yellow-red, large, and more or less swollen and hypertrophied.

2. f.sp. Tritici. -- In all essential respects the form which occurs on wheat, both in the uredo and in the puccinia stage, corresponds in respect to localization to the above-described form which is parasitic on rye, though perhaps in this case (Figure 113) the pustules are still more scattered over the whole blade of the leaf.

With respect to the shape and size of the uredo pustules this species, both f.sp. *Secalis* and f.sp. *Tritici*, is ordinarily quite well differentiated both from black rust and from yellow rust. Oddly enough, the pustules reach their greatest extent on the seedlings of the autumn (Figure 109), where they may have a length of 2 mm or even more. In the summer, on the other hand, their length (Figure 113 b) does not exceed 1 or at most 1.5 mm. The width hardly exceeds 1 mm. They are usually easy to distinguish from the uredo pustules of black rust by their small size. Like other uredo pustules, they open by bursting the upper covering pellicule (Figure 113 a), when the brown spore dust is freely exposed.

The color of those uredo pustules that occur on the leaves that the plant bears in the spring and summer is somewhat darker than the color of the pustules to be found on the seed leaves. It approaches the brown ochre color of the black rust uredo so closely that the two can hardly be distinguished. Let us mention here again that the content of the germ tube of a uredospore of this species is somewhat more strongly red than that of the yellow rust.

h. The Anatomical Structure

1. The Uredo Pustules and the Uredospores. -- In the structure of the uredo pustules no noteworthy difference has been observed from that of other similar pustules. As usual, the pustules follow the chlorophyll-bearing parts of the supporting surface, in this case exclusively such parts of the leaf blade (Figure 117 a). Nor do the uredospores (Figure 114) seem to differ from those of yellow rust, either in color, shape, and size, or in any other significant way. The dimensions were found to be as follows: for f.sp. Secalis: diameter 22-27 μ , or in cases where especially long ones were present, 24-28 x 22-24 μ ; for f.sp. Tritici: 18-26 μ or up to 22-29 x 16-22 μ ; and for the form occurring on Bromus secalinus: 22-25 μ . The membrane bears numerous somewhat separated spines, which appear to be arranged in quite regular rings. The germ pores are wide apart; their number is at least four. Sometimes between the uredospores we have observed thin, paraphysis-like fibers.

2. The Puccinia Spots and the Teleutospores. -- The teleutospore accumulations form almost exclusively on the under side of the leaf blade (Figure 117). These groups of spores, which are covered by the epidermis (Figure 118 a), are divided into many compartments, separated from each other by numerous brown (Figure 118 b) paraphyses, and each of these compartments contains only a few spores side by side. In the cell stratum below them there are numerous haustoria (Figure 119 b).

3. The Aecidia Spots and the Aecidiospores. -- In the examination of very young aecidia stages, so young that the spermogonia have hardly appeared, we have encountered under the epidermis a peculiar type of structures which are very reminiscent of those which Mæsse (I,47; plate IV, 1-2) found in studying the aecidia on Ficaria verna and which he regards as reproductive organs.

The aecidiospores are round or oval (Figure 123); their diameter is in the first case 20-30 μ , the dimensions in the latter case 20-30 x 19-22 μ . The membrane is thickly covered with small, warty spines.

1. The Economic Importance

This species of rust has no economic significance in Sweden to compare with that of black rust or yellow rust; it has been considered as fairly harmless, especially as it does not occur on any other parts of the host plant besides the blade of the leaf. How this may be in other countries is still to be investigated. The observations with regard to the sensitivity of various types of wheat to this species of rust will be reported in detail later.

5. Puccinia simplex (Kcke.) Eriks. & Henn. -- Dwarf rust.
Plate 41, Figures 124-128.

Diagnosis: I. Aecidium unknown (lacking?)

II. Uredo simplex. -- Pustules extremely small, 0.3 to 0.5 mm long, 0.1 to 0.2 mm wide, scattered in no order over the whole upper surface of the leaf, lemon yellow. Spores spherical to slightly elliptical, prickly, yellow, 19-22 μ in diameter or 22-27 x 15-19 μ .

III. Puccinia simplex. -- Groups of spores covered by the epidermis, forming on the underside of the leaf blade numerous extremely small point-like and on the sheaths somewhat longer black spots. Each group of spores divided into compartments by brown paraphyses, often much broadened at the tip. Spores pedunculate, for the most part unicellular, asymmetric, sacklike or stretched diagonally on one side, 24-30 x 16-18 μ , rarely two-celled, claviform, blunted at the tip or pointed sideways, 40-48 μ long, width of the basal cell 16-18 μ , of the terminal cell 19-24 μ .

Exsiccatae: Eriks., Fung. paras. scand. 120 (II, Smål., 15 August 1882) [see Note]. -- Linh., Ung. Pilze 127 (II, III, Hungary, June 1882). -- Rabn., Fung. Eur. 3214 b (III, Belgium). -- von Thüm., Herb. myc. 5 (II, III, Bohemia, September 1872); 6 (III, Bohemia, September 1872); 101 (III, Germany, 1867: F. Körnicke); Myc. univ. 831 (III, Denmark, 1876).

[Note] The form also appears in fascicle 9 of this work, which has recently been published, as no. 431 (Exp., II, "English early barley," 3 October 1891; III, "Six-row winter barley," 20 July 1892, and "Gray winter barley," 17 July 1890). --Late note, 18 September 1895.

Host plant: Hordeum vulgare (Sk., Alnarp -- Gotl., Dunegårda -- Exp.).

Historical: This form was first distinguished by Körnicke (according to Winter, I, 218) in 1865 under the name of Puccinia straminis var. simplex. Ten years later it was described by Nielsen (IV, 567) as Uromyces Hordei, and in 1876 by Rostrup in von Thümen's Herbarium Mycologicum Oeconomicum 451 as P. anomala. It is commonly assumed that P. Hordei Fuckel (I, 16) is synonymous with this, but the latter may be a different species, since the principal feature of P. simplex, the usually unicellular teleutospores, is not attributed to Fuckel's species. Fuckel's description as a whole rather suggests the conjecture that he may have been dealing with the form of P. glumarum that occurs on barley.

a. The Uredo Stage of the Fungus

Since this form of rust possesses only a very minor significance in this country economically, the attention that has been given to it has been relatively insignificant, and for that reason the contributions that have been offered toward describing its nature and developmental history are also few in number.

The uredo stage appeared on winter barley, which was sown at the same time as winter wheat, on seedlings in the late fall -- in 1891 on 9 October in two experimental plots, on 23 October on another, and on 27 October on another, and in 1892 on 6 October, 17 October, and 7 November on six plots -- as very small point-like pustules on the upper side of the leaf (Figure 124). An indication of the way in which this form spreads during the next 21 days over the leaf which it has attacked is given by Figure 54.

After the winter is over the uredo again appears in the spring or summer earlier, apparently, on winter barley than on summer barley. It was observed on winter barley

in 1892 on 27 May on 1 experimental plot,
on 29 June on 2 more experimental plots, and
in 1893 on 10 August on two experimental plots,

and on summer barley

in 1892 on 29-30 August on 17 experimental plots and
in 1893 on 4-5 September on 7 experimental plots.

Even then the pustules are very scattered and extremely small (Figures 125 and 126), incomparably smaller than in any of the forms of rust described previously. They are light yellow in color, rather like those of yellow rust. The spores (Figure 127) are round or somewhat oval. The germ tube that emerges from them in germination, as stated by Nielsen (VI,49) in 1877, appears to be often branched.

b. The Puccinia Stage of the Fungus

The teleutospore pustules also form pointlike spots, sometimes on the underside of the leaf and sometimes on the stem (Figure 128). These spots are black and are covered by the epidermis. The teleutospores are sometimes two-celled and sometimes one-celled, but the majority are the latter [see Note].

[Note] The form of rust that Körnicke (I,137) said he had found in 1865 on a barley plant from Persia and which had two-celled teleutospores is probably closely related to our P. glumarum f.sp. Hordei if not actually identical with it.

Attempts to bring these spores to germinate were made repeatedly in the autumn of 1892 in August and September, the last time on 29 September, but were not successful in a single case. In the spring of 1893 these attempts were resumed in May. The material, which had been taken from the experimental barn, where it had been kept over the winter, was inserted for germination on 8 May, but still showed no germination on 10 May. It was different with a sample that was taken from the experimental garden, where it had stayed in the open throughout the winter, and was inserted on 16 May. This sample showed a fairly general germination after 17 hours. But it was impossible to decide with certainty whether the one-celled spores had germinated. The tubes, which were pale in color, came from spores lying together in groups, so that it was not possible to distinguish each individual spore. Later in the same year, on 6 June and 14 June, the material from the experimental garden gave a negative germination result.

c. The Economic Importance

This species of fungus seems to have practically no economic importance at all in Sweden. In Denmark, on the other hand, as Rostrup (VIII, 66) states, it occurs in the ear, valves, and glume, as well as on the grains, causing these last to become "empty."

6. Puccinia coronata Corda. -- Crown rust. Plate XII, Figures 129-143.

Diagnosis: I. Aecidium Rhamni Gmel. -- Aecidia forming round or oblong yellow, more or less misshapen spots on the under-side of the leaf, especially along the nerves, on the calyx, and on the ovaries. Spores spiny, 18-25 x 14-19 μ .

II. Uredo coronata. -- Pustules sometimes long, up to 9 mm, and somewhat coalescent, sometimes very small, in some cases no larger than 0.3-0.2 mm in diameter, on the blade of the leaf, usually on the upper side, rarely on the sheaths, stems, valves, and glumes. Pustules reddish yellow. Spores spherical to slightly elliptical, spiny, yellow, 20-32 μ in diameter or 23-32 x 20-24 μ .

III. Puccinia coronata. -- Groups of spores commonly covered by the epidermis, at first often arranged in a ring formation around one or more uredo pustules, later forming black spots lying thickly strewn over the leaf. Groups of spores sometimes divided into a small number of compartments separated by brown paraphyses. Spores petiolate, usually somewhat claviform, cut off diagonally at the tip, with blunt projections of varying length arranged in a circle. The length of the spores 25-57 μ , width of the basal cells 8-19 μ , that of the terminal cells 10-19 μ .

Exsiccatae: I. Cooke, Fung. brit. 7 (Rhamnus cathartica and

Rh. Frangula, England, May 1865). -- Erb. Crit. Ital. 450 (Rh. Frangula, Italy, 1859); 1489 (Rh. Frangula, Italy). -- Eriks., Fung. nar. scand. 19 (Rh. Frangula, Drottningholm, 2 June 1891). -- Linb., Ung. Pilze 230 (Rh. cathartica, Budapest, May 1883); 329 (Rh. Frangula, Altenburg, summer, 1884). -- Syd., Ured. 62 (Rh. cathartica, Hungary, July 1883); 463 (Rh. Frangula, Germany, June 1890). -- von Thümen, Herb. myc. 212 (Rh. Frangula, Bavaria, June 1874); 266 (Rh. cathartica, Bavaria, June 1874); Mycoth. univ. 228 (Rh. Frangula, Bavaria, summer, 1874); 325 (Rh. cathartica, Bavaria, 1874); 933 (Rh. prinoides, Cape of Good Hope, October 1876); Fung. austr. 636 (Rh. Frangula, Bohemia, spring, 1872).

II and III: Eriks., Fung. nar. scand. 121 (III, Agrostis vulgaris, Små., 9 October 1882) [see Note]. -- Linb., Ung. Pilze 36 (III, Phalaris arundinacea, Hungary, 1882); 230 (II, III, Triticum repens, October 1883); 329 b (II, III, Glyceria spectabilis, Hungary, September 1884). -- Rabh., Fung. Eur. 692 (II, III, Avena sp., Germany); 3510 (III, Avena sterilis, France, June). -- Sacc., Myc. ven. 124 (II, III, Triticum repens, Italy, August 1874); 479 (II, III, Glyceria caustica, Italy, September 1875); 480 (II, III, Lolium perenne, Italy, September 1875). -- Syd., Ured. 120 (III, Glyceria spectabilis, Germany, 26 October 1879); 171 (III, Festuca alopecurus, Portugal, July 1889); 264 (III, Triticum repens, Germany, 1 November 1885); 272 (II, Aira flexuosa, Germany, July 1889); 315 (II, III, Hierochloa sp., Germany, August 1889); 364 (III, Holcus lanatus, Germany, August 1890); 563 (III, Avena hybrida, Germany, October 1891); 564 (Calamagrostis lanceolata, Germany, September 1891); 613 (III, Calamagrostis arundinacea, Germany, 25 September 1891). -- von Thümen, Fung. austr. 376 (III, Calamagrostis Epigeios, Austria, autumn, 1871; open pustules, habit similar to P. graminis); 377 (III, Avena sativa, Bohemia, autumn, 1872); 634 (II, III, Holcus lanatus, Bohemia, autumn, 1872); 945 (II, Holcus lanatus, Bohemia, summer, 1872); Herb. myc. 51 (III, Avena sativa, Bohemia, September 1872); 158 (III, Holcus mollis, Bohemia, October 1872); 311 (II, III, Festuca elatior, Germany, September 1875); Myc. univ. 1124 (III, Molinia coerulea, Germany, April, 1874).

[Note] In the recently published fascicle 9 this species also appears: No. 436, f.sp. Avenae (Avena sativa, Exp., II, 17 September 1890; III, 15 September 1892); 437, f.sp. Alopecuri (III, Alopecurus pratensis, Exp., 5 October 1894); 438, f.sp. Festuce (III, Festuca elatior, Exp., 5 October 1894); 439, f.sp. Lolii (II, Lolium perenne, Borgholm, 20 July 1894); 440 (II, Agrostis vulgaris, Borgholm, 20 July 1894); 441, f.sp. Calamagrostis (II, III, Calamagrostis arundinacea, Exp., September 1894); 442 a (C. lanceolata, Berg., II, 19 September 1894; III, 10 October 1894); 442 b (III, C. phragmitoides, Berg., 10 October 1894); 443, f.sp. Melicæ (II, Melica nutans, Exp., 23 September 1894).

Host Plants: I. Rhannus cathartica (Smål., Lyckås -- Öl., Borgholm, June 1886; A. Skånberg; -- Gotl., Visby, June 1891; G. Schotte -- Upl., Uppsala). -- Rh. Francula (Sk., Lund; E. Ljungström, I,120 -- Boh., Sälgvik; G. Lagerheim, I,151 -- Gestr., Gävle; G. Schotte, July 1891). -- Rh. grandifolia (Exp., artificial infection indoors; only spermogonia, but these in abundance).

II and III. Agrostis vulgaris (Smål. -- Hels., Ramsjö, 24 September 1891; uredo only). -- Alopecurus pratensis (Exp.). -- Avena sativa (Sk. -- Dal., Mora). -- Calamagrostis arundinacea (Exp.). -- Festuca elatior (Exp.). -- Lolium perenne (Sk., Lund; E. Ljungström, I,120 -- Exp.). -- Melica nutans (Exp.).

The following have also been reported as host plants of this species abroad:

I. Berchemia volubilis (Farlow & Seymour, I,15). -- Rhannus alnifolia (Farlow & Seymour, I,15). -- Rh. alpina (Saccardo, I,623). -- Rh. dahurica (Barclay, I,358, India). -- Rh. lanceolata (Webber, I,62, Nebraska, North America). -- Rh. oleoides (Cornu, II,182, France). -- Rh. utilis (Cornu, III,2, France).

II and III. Agrostis alba (Dietel, II,42, Germany). -- A. Hookeriana (Dietel, IV,230, India). -- Aira caespitosa (Dietel, II,42, Germany). -- A. flexuosa (Dietel, II,42, Germany). -- Andropogon Ischaemum (Voss, II,48, Carniola). -- Avena barbata (Lagerheim, III,8, Portugal). -- A. brevis (Kärnbach, I,10, Germany). -- A. elatior (Allescher, I,28, Bavaria; Schröter, III,324, Silesia; Dietel, II,42, Leipzig; Voss, II,48, Krain [Carniola]; Plowright, VI,164, England; Klebahn, I,340, Germany). -- A. fatua (Schröter, III,32, Silesia). -- Brachypodium silvaticum (Barclay, II,227, India). -- Bromus asper (Schröter, III,324, Silesia). -- Bromus inermis (Schröter, III,324, Silesia). -- B. mollis (Sorauer, II,223). -- Chrysopogon coeruleus (Dietel, IV,230, India). -- Cinna arundinacea (Webber, I,62, Nebraska; Farlow & Seymour, I,146, North America). -- Dactylis glomerata (Plowright, VI,164, England; Poirault, I, France; Klebahn, I,340, Germany). -- Festuca alopecuroides (Lagerheim, III,8, Portugal). -- F. arenaria (Nielsen, V,40, Denmark). -- F. arundinacea (Allescher, I,28, Bavaria; Farlow & Seymour, I,153, North America). -- F. distans (Schröter, III,324, Silesia). -- F. gigantea (Schröter, III,324, Silesia; Voss, II,48, Carniola; Barclay, II,227, India). -- F. littorea (Nielsen, V,40, Denmark). -- F. loliacea (Kärnbach, I,10, Berlin). -- F. ovina (Nielsen, V,40, Denmark). -- F. rubra (Nielsen, V,40, Denmark). -- F. silvatica (Schröter, III,324, Silesia; Plowright, VI,164, England; Klebahn, I,34, Ger-

many). -- Holcus lanatus (Allescher, I, 28, Bavaria; Körnbach, I, 10, Berlin; Schröter, III, 324, Silesia; Dietel, II, 42, Leipzig; Voss, II, 48, Carniola; Poirault, I, France). -- H. mollis (Allescher, I, 28, Bavaria; Schröter, III, 324, Silesia; Plowright, VI, 154, England). -- Hordeum vulgare (Nielsen, VI, 48, Denmark; Bolley, II, 7, Indiana; Pammel, I, 2, Iowa; Loverdo, I, 181). -- Lolium multiflorum (Schröter, III, 324, Silesia). -- L. spodiocum (Schröter, III, 324, Silesia). -- Lolium comratia (Dietel, II, 42, Leipzig). -- Phalaris amabilis (Allescher, I, 28, Bavaria; Schröter, III, 324, Silesia; Farlow & Seymour, I, 153, North America). -- Piptocarpha holciforme (Barclay, II, 227, India). -- Poa nemoralis (Voss, II, 48, Carniola). -- P. trivialis (Voss, II, 48, Carniola). -- Scolochloa festucacea (Körnbach, I, 10, Berlin). -- Secale cereale (Bolley, II, 7, Indiana). -- Triticum caninum (Schröter, III, 324, Silesia). -- T. glaucum (Webber, I, 62, Nebraska; Farlow & Seymour, I, 146, North America). -- T. repens (Schröter, III, 324, Silesia). -- T. vulgare (Burril, I, 200, Illinois; Bolley, II, 7, Indiana; Farlow & Seymour, I, 155, North America).

Historical. -- The aecidium stage of this fungus is described in 1791 by Gmelin (I, 1472) on Rhamnus -- species not given -- under the name Aecidium Rhamni ("theae cylindricis roseis, seminibus aurantiis" [with rose-colored thecae and golden seeds]), and ten years later by Persoon (II, 208) as Aecidium crassum. In 1803 Schumacher (I, 225) divided this aecidium into two species, one of which he called Ae. Frangulae ("ore integro" [with the mouth whole] on Rhamnus Frangula, the other Ae. Catharticae ("ore crenulato" [with the mouth crenulate] on Rh. cathartica). Just two years later Lamarck & de Candolle (I, 242, 244, 245) described no fewer than three Rhamnus aecidia, one called Ae. Rhamni-alpini, with circularly arranged sporecases, on Rh. alpina, a second called Ae. crassum on Rh. Frangula and Luonymus, and the third Ae. irregulare on Rh. cathartica. The last two bore spore cases which were grouped with no particular order and were distinguished from each other only by a somewhat different coloration of the aecidia. In 1825 Link (I, plate 2, 60) -- while at the same time criticizing Lamarck & de Candolle's differentiation of the forms -- himself set up a Caecoma crassatum on "Rhamnus species, Frunus spinosa, and other rosaceae," and a C. Rhamnatum on Rh. Frangula, the former of which he includes in a group that he calls C. incrassatum ("pseudoperidiis emersis" [with pseudoperidia turned upward]). A further grouping is found in Wallroth (I, 257), who in 1833 puts all Rhamnus aecidia down as a subdivision α) Rhamnorum of Ae. poculiforme on Berberis and on Phillyrea, a species of aecidia which also includes the aecidia on Luonymus.

Later we find the aecidia of the two common Rhamnus species sometimes separated again, as in Kick (I,4?) in 1867, who includes Ae. crassum on Rhamnus Frangula with a subspecies $\betadepauperatum which also occurs on the same Rhamnus species and sometimes on the same leaves as the main species, and Ae. Rhamni on Rh. cathartica and Rh. alpina.$

Next in time after the aecidiostage the puccinia stage was distinguished, first by Corda (I,6) in 1837 under the name Puccinia coronata, if we are to assume that although Corda states that his fungus occurred on the leaves of Luzula albida and draws it with very sharp points on the crown, he did have the same species of fungus before him that is called crown rust in these days on oats, rye grass, and other grasses. A few decades ago there were great misgivings about such an identification. For that reason in Belgium first Mathieu (I, 434) in 1853 and after him Westendorp (I,235) in 1854 distinguished the form of crown rust occurring on rye grass as P. coronata var. Lolii Bellk., characterized by blunt prongs on the crown. In Sturm's Flora von Deutschland (Flora of Germany) (I,5) Preuss in 1852 accepted a new species, P. serrata, with blunt prongs on the crown, which was said to occur on "the common cane" (? = Calamagrostis sp.), while Corda's P. coronata was "found in the same place on the leaves of barley." And apparently independent of the view of the two Belgian researchers mentioned, Nielsen (IV,551) in 1875 set up the crown rust of rye grass "tentatively" as a species to itself, Puccinia Lolii, beside P. coronata on "oats, barley, and other grasses." Two years later, however, Nielsen (V,39) no longer speaks of the new species, but counts the crown rust of rye grass with Corda's species.

In recent decades, in fact since de Bary's analysis of the main lines of the developmental history of the crown rust of grain (1866), although the above difficulties concerning identification have still not been entirely overcome, in general de Bary's procedure has been followed and all misgivings discarded, and the highly descriptive name Puccinia coronata has established itself, with Corda as its author, for the crown rust of cereal and grass species, with all the more justification because no one has since succeeded in finding a crown-bearing puccinia species on Luzula or in fact any other species of rust thus endowed than that of certain grass and cereal species, although the number of all puccinia species so far described now amounts to some 500.

Very recently Klebahn (I,340) in 1892 divided this species into two, P. coronata I (P. coronata in the narrow sense) on Dactylis glomerata and Festuca silvatica with aecidia on Rhamnus Frangula, and P. coronata II (P. coronifera) on Lolium perenne, Avena sativa, A. elatior, and Festuca elatior, with aecidia on Rh. cathartica.

On the same principles that we have followed in dealing with the species of rust described earlier (cf. pages 90 ff. above [i.e. in the original work]), we group the two species, as well as other little-known or unknown forms of crown rust on grasses, tentatively under the common designation Puccinia coronata.

The uredo form of this fungus appears to have been isolated at last. The first sure description of it is given by Fuckel (I,10) in 1860.

a. The Resting Stage of the Fungus During the Winter

Since this species of rust attacks only oats among the cereals, and since the winter oats, which cannot endure the winter in Sweden, has been grown only to a very insignificant extent in the experimental field, namely in the autumn of 1892 in one experimental plot of the field, and besides that in very small quantity in the experimental garden and among barberry bushes, we have had very little opportunity to observe and follow any occurrence of this species on seedlings in the late autumn. If we insisted on drawing conclusions from these few observations we should have to believe that this species of rust does not occur on the young plants in the late autumn, for at neither of the two plantings mentioned was it possible to discover even a trace of Uredo coronata, although this species of rust occurred quite abundantly on the adjacent summer oats plots of the experimental field, and on neither of the two places was the winter oats able to endure the winter cold.

It was otherwise in the autumn of 1891 with the seedlings of summer oats that had sprouted up at that time on the experimental field from grains dropped there. Several of these seedlings in addition to the black rust uredo bore Uredo coronata as well, and this uredoform could be found as late as 24 October, and on plants that were transplanted from the experimental garden even as late as 5 November. Since all such plants freeze with the onset of winter, even this finding can offer no proof for the assumption that crown rust winters in the uredoform on oats.

This does not exclude the possibility, however, that this is the mode of spending the winter in other forms of this species of rust which occur on certain wild or cultivated perennial grasses. The conjecture that there is such hibernation in several of them is found here and there in the relevant literature. Thus Kuhn (II,401) says in 1875 that crown rust lives through the winter in the uredoform on Holcus lanatus, for "in the middle of the winter the uredoform is found in all stages of development in fall sproutings of this grass," and he even adds, "the uredoform that has lived through the winter develops further uninhibitedly in the

spring." Von Thümen (II,24) says the same thing in 1896 about crown rust: "uredospores also live through the winter, chiefly on species of grass that grow wild, and the young oat crop is then infected by them in the spring." But Barclay (II,228) expresses himself most circumstantially, when he says in 1891 that in India in the Puccinia coronata var. himalensis on Piptatherum holciforme and Festuca gigantea the uredo pustules are to be seen "in abundance throughout the winter in shady places and in the beginning of spring on tender, still undeveloped leaves." The cause of this phenomenon in his opinion lies "either in an uninterrupted production of uredo throughout the year" or on "the mycelium's surviving in the root." Barclay himself, however, calls the first assumption "an improbable hypothesis," and as to the second he states that "in the microscopic examination of the root no hyphens have been found," though at the same time he mentions experiments that make this assumption probable to him. "At the beginning of the spring a plant with dry leaves bearing numerous teleospores was dug out of the ground and the plant was kept in a laboratory with its roots in water that was regularly replenished. After a short time the plant developed new green leaves, and on 17 May a few uredo pustules were found on one of them, thus showing in an almost decisive way that the mycelium is perennial."

To get a more detailed knowledge of how it may be here in Sweden in this respect, in the autumn of 1891 we planted a number of wild grasses that bore uredo in the experimental garden and examined the planted individuals several times in the course of the winter. The results of these observations are shown in Table 46, where 0 represents the absence and 1 the presence of uredo pustules on the plants observed.

Table 46. Uredo coronata on Several Species of Grasses in the Experimental Garden in the Winter of 1891-1892

No.	Species of Grass	Date of Observation											
		21 10	13 15	11 11	24 20	31 31	7 7	14 14	20 20	27 27	31 31	7 7	14 14
1	<i>Agrostis vulgaris</i>	1	1	.	0	.	.	.	0	0	0	0	0
2	"	1	1	.	1 ¹	.	0	0	0
3	<i>Alopecurus pratensis</i>	1	1	0 ²	.	.	0	0
4	<i>Calamagrostis arundinacea</i> ³	1	1	1	.	.	0	0 ²	.	0 ²	.	0	0
5	<i>Festuca elatior</i>	1	1	.	.	.	0	0 ²	.	0	0	0	0
6	"	1	1	.	1 ⁴	0
7	<i>Lolium perenne</i>	1	1	1	1	†	.	.	.
8	<i>Melica nutans</i>	1	1	0	.	.	0

Notes: 1) On withered leaves generally. — 2) Some green leaves were to be found. — 3) Whether the form on these host plants really belongs to Puccinia coronata is not quite clear. — 4) New leaves rustfree; uredo general on withered ones.

In no case did we succeed in finding a single new uredo pustule on the transplanted plants in the new year, at least before the end of May, although by that time and in several cases even one to two months earlier green leaves occurred generally. These observations thus do not attest the hypothesis that the uredo lives through the winter on wild grasses.

Meanwhile during the same winter on one of the species of grass indicated here, Melica nutans, growing outdoors in the woods of the experimental field (at the Sjöstugan), the uredoform was found on withered, crumpled leaves not only on 31 November [sic] but also on 5 April, still capable of germinating on the latter date, and on 27 May fresh uredo pustules were to be seen on newly sprouted leaves at the same spot. The next winter, too, uredo capable of germinating were found on withered leaves of this grass on 1 December 1892. Germinating experiments with material taken from the same place on 18 March the next year were unsuccessful, however, as no germination had taken place after five days.

b. The First Generation of the Fungus: the Promycelium Stage

1. The Germinating Season of the Teleutospores. -- As to the time when the teleutospores germinate, de Bary (V, 211, 213) says in 1866 that germination takes place "after hibernation," early in the spring, and that "at the end of the spring no ungerminated spores capable of germinating are to be found outdoors." The same opinion is expressed in all the more recent publications as well. And from India Barclay (II, 230) writes in 1891 that the teleutospores of the form which occurs on Brachypodium silvaticum germinate after the winter has run its course, "from the end of March until August," but those of the forms which occur on Piptatherum holciforme and Festuca elatior "earlier, in the laboratory as early as 15 February."

At the experimental field in October 1891 the capability of the teleutospores of the forms occurring on Festuca elatior and Calamagrostis arundinacea to germinate was tested in numerous experiments, but always without result. At the beginning of May of the next year, however, the spore material taken from Festuca elatior showed rapid and general germination after only 24 hours, as did the material obtained from Alopecurus pratensis. Generally the germination of both forms was on 25 May that year. In the last-mentioned cases the material had stood outdoors throughout the winter. In the spring of 1893 the teleutospores generally germinated on 25 May after 16 hours in the form on Avena sativa, which had also been outdoors over the winter, and its germination lasted until 2 July. After that day, on the other hand, the germination results were poor, probably because the majority of the spores had already germinated before they were inserted for germination.

2. The Course of the Teleutospore Germination. -- When the teleutospores germinate, a germ tube, in the usual way, generally first emerges from the terminal cell (Figure 135) and then also from the base cell in the form of a thick, strong thread. From the terminal cell the germ tube pushes out between the prongs of the crown, from the base cell directly beneath the partition wall. The content of the promycelium, like that of the sporidia, as de Bary (V, 211) noted in 1866, is yellowish red in color. But here, as in the germination of the teleutospores of black rust (cf. page 56 above [i.e. of the original work]), sometimes no sporidia formation takes place. Only a long protruding, much branched, sterile promycelium develops (Figure 138).

Because of its strongly yellow-red colored sporidia this species is very well suited to microscopic studies of the course of the sporidia formation. Accordingly, in the spring of 1893 very numerous studies of this species were done, some on a glass disk as a base, and some on strips of epidermis taken from rhamnus and oat leaves. In the experiments done on the glass disk (Figure 140) a germ tube of varying length usually developed. In the experiments on a living base, however, the germ tube showed a definite reaction to the base; this was just as unmistakable when the base was taken from an oat leaf as from a rhamnus leaf. As soon as the tube had reached the wall of a cell beneath it, its growth in length ceased. If the underlying layer of cells was the epidermis of Rhamnus cathartica, the tube bored directly through the epidermis wall with its tip and emptied its colored contents into the hollow of the epidermis cell in an irregularly branched thread (Figure 141). Sometimes hardly any germ tube developed, but the pointed end of the sporidia forced its way in directly in the same way.

The reaction of the sporidia thread or of the sporidia to the underlying strip of epidermis from an oat leaf (Figure 142) was also very peculiar. Here again a rapid pouring out of the colored contents took place without the previous formation of a germ tube (Figure 142 a). In several cases it even appeared as though this outpouring were connected with a boring through the epidermis wall. We did not reach complete certainty in this matter, however, since at the beginning of July, when these experiments were in full swing, the germination of the spores began to decrease and finally stopped altogether. It should be superfluous to point out how important it is to achieve complete certainty concerning this phenomenon, for here lies the solution of the question, both theoretically interesting and practically important, of whether a direct sporidia infection of the hosts of the uredo and teleutospores actually occurs in this species, and in that case probably in other heteroecious uredineae.

In some cases the development of secondary sporidia was also observed in this species (figure 142 b).

3. Infection Experiments with *Puccinia coronata*. --

The first successful infection experiments with sporidia of this species that are mentioned in the literature are those of de Bary (V,211) in 1865. The species of the host plant from which the teleutospores were taken is not given, but the assumption that it was one of the *Poa* species is probably not unjustified, since *Holcus* is mentioned as the only kind of grass on which this fungus "is found by preference outdoors." An inoculation done on 25 May on *Rhamnus frangula* produced yellow spots on the inoculated parts of the leaf after 10 days and spermatogonia and aecidia shortly afterwards. After that time as far as we know no infection experiments of that kind are mentioned until toward the end of the eighties. Flourens (VI,164) in 1889 reports that in numerous cultures he produced aecidia with teleutospores from *Dactylis glomerata* and *Festuca silvatica* on *Rhamnus frangula*, but never on that host plant when he got the material from *Lolium perenne*.

At about the same time Barclay (II,232) carried out his experiments in India with the forms that occur there. The first of these experiments was done in 1889 on 25 June with material that had been taken from *Brachypodium silvaticum* on *Rh. dahurica*. After nine days numerous spermatogonia had appeared, and after 29 days young aecidia. In 1890 Barclay did ten infection experiments on the same *Rhamnus* species from 11 April to 2 July with material that he had gathered from 16 January to 5 February, partly from *Brachypodium*, partly from *Piptatherum*, and partly from *Festuca*. The three inoculations with material from *Brachypodium* in particular yielded beautiful positive results, -- spermatogonia beginning after 5-6 days and finally aecidia in two cases on 27 of 52 inoculated leaves, and in the third case "numerous aecidia spots on a number of leaves." The experiments done with material gotten from *Piptatherum* had a somewhat inferior result (4 cases), for only 15 of 64 inoculated leaves gave a positive result, and this was also true of the experiments done with the material gotten from "*Piptatherum* or *Festuca*" (3 cases). Barclay is of the opinion that these experiments prove the relationship of the form on *Brachypodium* to the aecidia on *Rh. dahurica*, but says that the relationship of the forms occurring on the other grasses to the aecidia of the *Rhamnus* species mentioned was not satisfactorily shown. And if there is in fact a relationship here, it is still odd that the forms from the last-mentioned species of grasses are so much harder to grow, and that this difficulty manifests itself in the fact that when infections are done with them the cycle goes no further than the development of spermatogonia.

Lastly we must give our attention to the experiments

Table 47. Infection Experiments with *Uromyces caryocarpae*

Exp. No	Date	Infectious Material		Spots Infected		Result		Incubation Period of					
		Origin	Germinating Capacity of Infectious Material	Plants Infected Species	Number	Position	Number of Spots of Infection Broken Out	Sper- mo- gonia	Acidia	Days			
1	1892	<i>Festuca elatior</i>	18	<i>Berberis vulgaris</i>	1		-						
2	"	"	24	<i>Rhamnus cathartica</i>	1	Buds	+		6	22			
3	"	"	17	<i>Anemone arvensis</i>			-						
4	"	"	21	<i>Rhamnus Frangula</i>		Buds	-						
5	"	<i>Alopecurus pratensis</i>	72	" cathartica	1	12	+		10				
6	"	"	18	"			+		9				
7	1893	<i>Avena sativa</i>	4	16	"	<i>Fraxinus</i>	1	27	Leaves	-			
8	"	"	"	"	"	cathartica	1	20		+	17	7	14
9	"	"	"	"	"	Fraxinus	1	28		-			
10	"	"	"	"	"	cathartica	1	24		+	14	6	13
11	"	"	"	"	"	grandifolia	1	18		(+)	7	6	
12	"	"	"	"	"	alnitolia	1	21		(+)	1		
13	"	"	"	"	"	cathartica	1			+			

Notes: 1) Spermogonia developed very abundantly and strongly, but no acidia developed. -- 2) Spermogonia very scanty, on only one spot. -- 3) The whole plant was sprinkled with water containing sporidia, and as a result the whole plant became covered with rust.

carried out very recently by Klebahn (I, 340) with the teleutospores of *Lolium perenne* on two specimens of *Rh. Fraxinosa* and two of *Rh. cathartica*, where only one experiment on one plant of the last-mentioned species had a positive result.

The infection experiments at the experimental field with teleutospores of this species are summarized in Table 47.

If we examine this table closely we find the following:

With transfer of material		Number of infections with results		
from	to	definitely positive	doubtfully positive	definitely negative
		+	(+)	-
<i>Festuca elatior</i>	<i>Rhamnus cathartica</i>	1		
" "	" <i>Frangula</i>	.	.	1
" "	<i>Berberis vulgaris</i>	.	.	1
" "	<i>Anchusa arvensis</i>	.	.	1
<i>Alopecurus pratensis</i>	<i>Rhamnus cathartica</i>	2		
<i>Avena sativa</i>	" "	3		
" "	" <i>Frangula</i>	.	.	2
" "	" <i>grandifolia</i>	.	1	
" "	" <i>alnifolia</i>	.	1	

In other words, from the three species of grasses there was one positive result on *Rh. cathartica*, and from two of them negative results on *Rh. Frangula* [see Note].

[Note] For later series of infection experiments see Eriksson, V, 317, and Klebahn, III, 129 ff., and IV, 151. --Late note, 18 Sept. 1895.

c. The Second Generation of the Fungus: the Aecidium Stage

The time indications in the relevant literature with regard to the appearance of aecidia on *Rhamnus* species are relatively very few in number. From Europe we know of none besides de Bary's (V, 213) from 1866, where he says that they develop "only in the spring," and Nielsen's (IV, 554) from 1875, where he says that "the spring is their flowering season." In India, as Barclay reports in 1887 (I, 358) and 1891 (III, 227), the aecidia on *Rh. dahurica* "are completely mature in the last half of May, but more commonly in the middle of July." Here in Sweden this aecidium appears to come out at about the same time as that on the barberry. A beginning of spermatogonia formation on *Rh. cathartica* was observed at the experimental field in 1895 on 3 June and open aecidia on the same host plant in Uppsala on 12 June in 1892. Abundantly developed aecidia were collected from the same *Rhamnus* species at the Kinckulle (on Väner lake) on 16 June 1889.

There were no results from the first experiments that de Bary (V, 212) did in 1865 to produce rust on oats and other cereal species with aecidia spores from *Rhamnus Frangula*; this has now found its natural explanation, since it has been proved that the crown rust of oats is not to be associated with the aecidium on *Rh. Frangula*, but with that on *Rh. cathartica*. Nielsen (IV, 550) had better success in his experiments with aecidiospores from *Rh. cathartica* which he transferred

to rye grass. These experiments done on 16 June produced uredo spots after nine days. Parallel experiments with aecidiospores from Rh. cathartica, on the other hand, had a negative result. Nielsen obtained the same result in 1877 (V,39) after repeated experiments. In 1890 Cornu (II,181) mentions experiments with aecidiospores from Rh. cathartica which he inoculated on oats, obtaining a positive result after 21 days, and also successful experiments with aecidiospores from Rh. olcoides. Lastly, Klebahn (I,338) obtained uredo on 16 June and puccinia in August with aecidiospores that he transplanted on 2 June (1892) from Rh. cathartica to Lolium perenne. We have had no opportunity ourselves to carry out successful experiments with the aecidiospores of this species of rust [see Note].

[Note] For new infection experiments see Eriksson, V,325 and 319 and Klebahn III,129 ff. and IV,152. --Late note, 18 September 1895.

d. The Third Generation of the Fungus: the Uredo Stage

1. Time of Appearance. -- The mentions of the first appearance and the actual period of flowering of this fungus in the uredo stage are very brief. From Europe, as far as we know, only two reports are available, an older one from Nielsen (IV,552) of 1875 to the effect that "at the end of June or somewhat later rust begins to be general (in Denmark) on rye grass, but it is not until August and September that its attacks become really noticeable," and a later one from Plowright (VI,165) of 1889 to the effect that the form parasitic on Lolium perenne develops "an abundance of uredospores" in England, "but only in the autumn, from September to November," while on the other hand the form on Dactylis glomerata is "an early summer species with a much more scanty development of uredospores." In India, according to Barclay (II, 228), 1891, uredo pustules of the Indian form or forms of this species develop "at the beginning of the spring on young, still undeveloped leaves, even before leaves can be seen on Khamnus."

The observations concerning the times of appearance of this uredo form that we have had an opportunity to make are shown on Table 48 below.

It will be seen from these observations, scanty as they are, that this uredo form, at least on oats, does not appear until late in the summer, and perhaps even later than black rust on the same species of cereal. It will also be seen that both the appearance and the peak season vary in different years. This rust was very profuse in 1890 ("a crown rust year"), less numerous in 1892, and very scanty in 1893 [see Note].

[Note] On variation in individual years see also Eriksson, V,323.

--Late note, 18 September 1895.

Table 48. *Uredo caricis* on Cereals and Grasses in the Season of 190-33

Year	Experimental Field	No. of Rusty Expts. Plots from	Experimental Station		Hesperia	
			Presence (1) or Absence (0) of Rust on	Presence (1) or Absence (0) of Rust on	Presence (1) or Absence (0) of Rust on	Presence (1) or Absence (0) of Rust on
1890	Avena sativa	1-1-1				
1891	Cultivated field	1-1-1	Urtica dioica			
			Urtica dioica	1-1-1		
1892	Cultivated field	1-1-1	Agrostis vulgaris	1-1-1	1-1-1	1-1-1
			Urtica dioica			
1893	Cultivated field	1-1-1	Urtica dioica			
			Avena sativa			

Notes: 1) In 1891 the oat crop at the experimental field did so badly that it was not worthwhile making further observations. -- 2) At Hesperia on new leaves. -- 3) On the experimental field near the railway station.

2. Germinating Capacity of the Uredospores. -- The European literature appears to contain no information concerning the germinating capacity of the uredospores and the course of their germination. Barclay (II, 229) in 1891 is speaking only of the germinating capacity of certain Indian forms when he says that the uredospores of the forms on Piptatherum and Festuca retain their capacity to germinate for a long time, in one case from 16 January to 2 June, or about 4 1/2 months. These spores were on dry leaves with numerous puccinia but only a few uredo pustules; the leaves were gathered on 16 January and cut into small pieces, and were then kept in beakers lightly covered with watchglasses, in a room. On 2 June they were scraped off and kept in a moist atmosphere, and after 24 hours they germinated well.

In the experiments done with these uredospores at the experimental field the germinating capacity always proved to be good. The germ threads showed up after only a few hours. Even after freezing the germinating capacity was good; thus these spores germinated generally after 23 hours -- some even beginning to germinate after only four hours -- on 26 and 27 October 1891 after previous freezing nights.

3. Infection Experiments with Uredo Caricis. -- Infection experiments with uredospores of this species of rust are mentioned only by Nielsen (II, 190) in 1875, where he says that after inoculation with the uredo from eye grass on oats he obtained uredo on the inoculated parts of the leaves in seven days and beginning puccinia on the underside of the leaves in fourteen days. The experiments done at the experimental

Table 49. Infection Experiments with Puccinia pratensis

Infection No	Date	Infectious Material		Plants Infected		Placers Infected	Result
		Origin	Germinal- ing. Cap- ity	Species	Number		
1	1891	<u>Calamagrostis arundina- cea</u>	25	<u>Avena sativa</u>	2	leaf tips	—
2	1891	<u>Calamagrostis arundina- cea</u>	25	<u>Avena sativa</u>	3	leaf tips	—
3	1891	<u>Avena sativa</u>	4	<u>Avena sativa</u>	2	leaf folds	1
4	1891	<u>Avena sativa</u>	4	<u>Trifolium pratense</u>	2	—	—
5	1891	<u>Alonecurus pratensis</u>	1	<u>Avena sativa</u>	3	leaves	—
6	1891	<u>Melica nutans</u>	3	<u>Avena sativa</u>	3	—	—

Note: 1) Pale spots appeared at the points of infection: 1 after 17 days, 3 after 19, and 4 after 21 days, but even after 25 days no uredo pustules had come out.

field from 1891 to 1893 are shown in Table 49.

As the table shows, in no case did the transfer of spores from Alonecurus pratensis, Calamagrostis arundinacea, and Melica nutans to oats succeed, and only one infection experiment from oats to oats yielded a positive result.

4. Puccinia coronata a Collective Species. -- There is no doubt that in this species, too, there is a specialization of the forms on the various host plants that is analogous to that which we have encountered in the species discussed earlier, even though the infection experiments on which a correct differentiation of the forms must be based are much too few in number in this case for a correct differentiation of forms of the species as a whole to be done. Meanwhile we are perhaps justified on the basis of the experiments done both with teleutospores and with acidiospores as well as with uredospores in assuming for the time being the following classification of the forms:

Series I. Accidium on Rhamnus cathartica (?Rh. oleoides, Rh. grandifolia) [Puccinia coronifera Kleb.]:

f.sp. Avenae on Avena sativa and Lolium perenne,
f.sp. Alonecuri on Alonecurus pratensis,
and the forms on Festuca elatior and Avena elatior.

Series II. Accidium on Rhamnus Frangula [Puccinia coronata I Kleb.]:

the forms on Doctylis glomerata and Festuca silvatica (? Pucc. gibberosa Lagerheim, IV, 124).

Series III. Ascidium on grasses, *Securaria* [*Puccinia*
gracilis var. *gracilis* (Pers.) Berk.]
the forms on *Phalaris intermedia*, *Phalaris holciflora*
and *Lectuca pinnatifida*.

Series IV. Those forms concerning whose possible relationship to any of the aforementioned or other *Uromyces* species or concerning whose possible lack of an ascidium stage we know nothing at all as yet:

f.sp. *Calamagrostis* on *Calamagrostis arundinacea* and
f.sp. *Malicea* on *Malicea nutans* (see Note).

[Note] Concerning the specialization of this species according to the latest experiments of 1894 see Eriksson, V, 321. --Late note, 18 Sept. 1895.

e. The Fourth Generation of the Fungus: the Puccinia Stage

The uredo stage of the fungus is very quickly followed by the puccinia stage. Nielsen (IV, 593) found in 1874 that in his infection experiments with the uredo from rye grass on oats it followed 14 days after the infection. At the experimental field the puccinia stage was found on oats in the field on 19 August 1890, and in infection number 3, Table 49, on 23 October 1892, 26 days after the uredo infection, and on *Agrostis vulgaris* in the experimental garden on 27 September 1892.

f. The Cycle of Development

The developmental cycle of the fungus, according to what we can see from the facts available, should correspond in the main to that of *Puccinia gracilis* (cf. page 107 above [i.e. in the original work]), except that the name *Rhamnus* must be substituted for that of *Berberis*. Scattered observations concerning the more or less abundant occurrence and even at times the almost complete absence of this or that spore form on the host plants, however, make it probable that the developmental cycle of the forms occurring on the various species of grasses may be not insignificantly different. Thus Plowright (VI, 165) in 1889 points out a difference between the form on *Lolium perenne* and that on *Dactylis glomerata*, which manifests itself in the late and abundant occurrence of the uredo stage in the former and in the early and scanty occurrence of it in the latter. We have encountered the form on *Malicea nutans* almost exclusively in the uredo stage; only once, on 13 November 1891, has it been possible to find the puccinia form, in that instance on a chenth [see Note]. In one case, too, the form occurring on *Agrostis vulgaris* was much suppressed in the ascidium stage. In some specimens of this grass that were collected on 27 September last near Ramö in Helgeland the teleosporoes were lacking on nearly withered leaves which were almost completely covered with uredo pustules.

[Note] On f.sp. *Malicea* cf. also Eriksson, V, 324. --Late note,
18 September 1895.

g. The Localization of the Uredo and Puccinia coronata

When the form on Trigonotis appears in the uredo stage in the summer, it either forms more or less lengthwise extended, somewhat coalescent pustules, up to 9 mm in length (Figure 129 b), or else the pustules are smaller, 2-3 mm long, and more scattered (Figure 129 a). They may occur on both sides of the leaf, but most numerous on the upper side. They are red-yellow in color, most closely approaching the yellow rust of wheat, and differ in color from the uredo of black rust, which is much darker. The difference in color between the uredo of crown rust and that of black rust comes out most clearly on leaves (Figure 129 a) on which both are present. In general the uredo reaches a very great expansion on the leaf once attacked by it, since it takes up the greatest part of the blade of the leaf. Meanwhile the puccinia stage begins to appear as a dark ring around the uredo spots. This ring, which at first is very small (Figure 131 a), gradually enlarges, its color changing to the purest black (Figure 131 c). Under the magnifying glass it is evident that the dark ring consists of covered puccinia pustules (Figure 132). These spore pustules differ from those of the black rust in being covered (Figure 131 b, at x). Finally no yellow uredo is visible any longer, the leaf being densely covered with scattered black spots (Figure 131 d).

It is a striking fact that the fungus, at least here in Sweden, appears almost solely on the blade of the leaf. Only in the year 1890, which was especially favorable to the growth of the crown rust on oats, were there a few cases in which it appeared as open uredo pustules on the inside of thecal valves.

On other host plants, too, this rust seems to occur either solely or at least by preference on the blade of the leaf. Seldom have we observed rust spots on other parts of the plant, as e.g. on sheaths of Alopecurus pratensis, Melica nutans, and Festuca elatior, or even on stems as in the case of Alopecurus pratensis. In the form parasitic on Melica the uredo forms more or less densely placed yellow, round pustules, with a diameter of 0.2-0.3 mm, commonly with short, light yellow stripes in the lengthwise direction of the pustules. A ring formation of teliospore groups around the uredo pustules hardly occurs in the spots that appear on Calamagrostis arundinacea and Agrostis vulgaris [see Note].

[Note] For the localization, cf. also Klebahn, III, 135, 136, and Plate III.
--Late note, 18 September 1891.

h. The Anatomical Structure

1. The Uredo Pustules. -- In the oats form the structure of the uredo pustules seems to be the same as in the

species described earlier, and here as usual the continuous nerves (Figure 128) form an obstructing wall that the mycelium cannot penetrate. It can be seen from cross sections that the development of the aeciospores is limited to the central parts of the mycelium, while the teleutospores develop in the peripheral parts. The aeciospores of the form growing on oats are spherical or slightly distended toward one side and are prickly (Figure 130), 20-32 μ in diameter, or if elongated, 28-32 x 20-24 μ . For purposes of comparison let us mention here that the dimensions of the spores are variously given. According to Winter (I, 219) 1886 and Saccardo (I, 623) 1888 they are 19-28 x 16-21 μ ; according to Burrell (I, 200) 1885, 21-24 x 18-21 μ ; according to Schröter (III, 324) 1887, 20-24 x 17-20 μ ; according to Howland (VI, 164) 1889, 20-28 x 15-20 μ ; and lastly, according to Barclay (II, 231) 1891, in the form on Brachypodium sylvaticum 20-24 x 15-21 μ , and in the form on Piptatherum holciforme 22-33 x 20-32 μ .

2. The Puccinia Spots and the Aeciospores. -- The origin of the puccinia spots of this species is described by Bolley (I, 177) in 1889 as follows: "Several ordinary mycelium threads meet and merge together in an intercellular space which lies immediately beneath the epidermis and is filled with abundant protoplasm. From the upper stratum of this spore-storage compartment the spores emerge as originally short, thick protuberances, which gradually develop into thin-walled, sack-like bodies. They are divided quite early by a partition wall into a lower part (the stem) and an upper part (the spore). Later the spore itself divides with a transverse partition approximately in the middle, whereupon its walls become thick and brown."

When fully developed the spores, as indeed is generally reported in the literature, are as a rule covered by the epidermis lying above them (Figure 135 a). It more rarely happens that these bunches of spores form uncovered, open pustulae, as in black rust. Such a case is first mentioned by Barclay (II, 230) in 1891 in a description of the Indian forms of the fungus. He says that the form occurring on Brachypodium sylvaticum possesses small, point-like, quite bare bunches of teleutospores on the upper side of the leaf, while on Piptatherum holciforme and Festuca gigantea they are found to be linear and more or less covered and are on the under side of the leaf.

At the experimental field open puccinia pustules were observed on Piptatherum holciforme on the upper side of the leaves on 19 October 1892 which were generally about 2-5 mm long, while the spots occurring on the sheaths were small, covered, almost point-like, and arranged in rows, approximately as in Puccinia glumarum. On leaves of Piptatherum holciforme open puccinia pustules were found on 19 October 1892, and on a

sheath of Helicium nutans on 13 November 1891.

Ordinarily in the description of the species in the relevant literature there is no mention of occurrence of paraphyses between the teleutospores, or, as in Schröter (III, 324) 1887 and Saccardo (I, 623) 1888 this is attributed to the puccinia forms, which lack paraphyses. In view of this it is odd that at the experimental field paraphyses have been observed in the form occurring on oats (figure 135 a). To be sure, where they appeared at all (figure 135 b) they did not occur on quite so many places in the groups of spores as in the case of yellow rust or brown rust, but they were nevertheless numerous enough not to escape notice.

The spore-generating mycelium, as usual, is chiefly intercellular (Figures 133 a, 134 a), the branches numerous, intertwined with each other (Figure 134 b), the form of the adjacent leaf tissue cells being quite well preserved. There are also haustoria inside the cell.

It has already been mentioned above that Corda (I, 6) in 1837 wrote that his then new species Puccinia coronata occurred on Luzula albidula, and that he pictured the species with sharp prongs on the crown. But since no such form has been encountered again since, we may perhaps be justified in the assumption that Corda's identification of the host plant was incorrect and his drawing not quite true to nature. In all later investigators, e.g. Westendorp (I, 235, Figure 2), 1854; Preuss in Sturm (I, Table 3 c), 1862; Nielsen (IV, Figures 11 and 14), 1875; Frank (I, 457), 1880; Sorauer (I, Plate IX, Figure 3), 1886; Brunchorst (I, 106, Figure 16 b), 1887; Plowright (VI, Plate IV, Figure 3), 1889; Barclay (I II, Plate 56, Figures 8-13), 1891; and Loverdo (I, 182, Figure 18), 1892, the prongs of the crown are described and pictured as blunt, just as in our Figures 135-137 on Avena sativa and Figure 143 on Festuca elatior.

The dimensions of the teleutospores according to Winter (I, 219), 1880, and Saccardo (I, 623), 1888 are 35-60 x 12-21 μ ; according to Burril (I, 200), 1885, 45-55 x 15-18 μ ; according to Schröter (III, 324), 1887, 40-60 x 13-17 μ ; according to Plowright (VI, 164), 1889, 40-60 x 12-20 μ ; and according to Barclay (III, 231), 1891, in the form on Brachypodium silvaticum 38-44 x 10-11 μ and in the form on Piptatherum holciforme 43-55 x 8-14 μ . At the experimental field the dimensions were as follows:

on	length	width of basal cell	width of terminal cell
<u>Avena sativa</u>	38-57 μ	11-15 μ	12-14 μ
<u>Agrostis vulgaris</u>	25-33 μ	10-19 μ	12-19 μ
<u>Helicium nutans</u>	31-45 μ	8-14 μ	10-12 μ

i. The Economic Importance

Sometimes great importance is ascribed to this fungus from the economic point of view. From Denmark, for example, Nielsen (IV,553) writes in 1875 that in August and September of the two previous years he "had seen many very bad rustures looking scorched," and upon "closer examination" had found that the young rye grass plants were so infested with this species of fungus that it appeared as if the "grass were completely withered." At the same time he expressed the view that "no other species of rust destroys the leaves of its host plant with greater rapidity" than the crown rust of rye grass. Great damage to the same species of grass in Denmark was later mentioned by Rostrup (V,13), 1835, (VI,8), 1836, and (VIII,5), 1838; he also reports the peculiar phenomenon that in the three years (1834, 1835, and 1837) for which the reports speak, the rye grass grown from Scotch and Irish seed suffered far worse than that from Danish seed, even where they were growing side by side. The former was "heavily sprinkled with yellow rust," sometimes so much so that the boots of anyone who walked across the field became "quite red," while the latter appeared "fresh and green" or only "insignificantly" infested with rust.

Heavy damage caused in Holstein by this species of rust on oats is mentioned (Presse, I,748) for the year 1891, when he says that the advent of this species of rust was given by the farmers as in the time around St. Bartholomew's, 24 August, that the rust caused a collapse of the leaves and stems, -- "Bartholomew struck down the oats with his club" -- and that the weight of the grain was thus reduced from 150 pounds per Holstein bushel to 96 pounds. As shown by samples and reports sent in by the head of the county constabulary, Mr. J.A. Hansson, heavy damage was done by this species of rust to the oats in the Tanums-Bärad in Bohus county about 27 August 1890, when "almost every blade of oats was infested there like the sample sent in." The rust does not appear to have done "any noticeable damage to the kernels," as we learn from a later letter of 2 March 1891.

A varying sensitivity to this species of rust in varieties of oats has been discussed only once, as far as we know, namely in von Sievers (I,361), in 1837, who says that of numerous varieties of oats grown by him only one, "the Russian Orel oats grown in Rümershof," was almost immune. All the others were susceptible to about the same degree. At the experimental field we have not been able to demonstrate any varying susceptibility of individual varieties of oats to this species of rust.

B. Contributing (Secondary) Causes

Although it is now an undisputed fact that the rust of grain is primarily conditioned by the rust fungus forms just described, which might be described as the original or primary causes of disease, on the other hand it is just as indisputable that several other factors contribute to the greater or less destruction caused by the fungus. We shall now discuss these under the general rubric of contributing or secondary causes of disease; indeed, from the practical point of view it is precisely these causes of disease that deserve to be given preferential consideration, since it depends on them whether a year becomes a rust year or not. We call these

a) External Contributing Causes of Disease,

Including 1) the location and drainage, 2) the physical nature of the soil, 3) the chemical composition of the soil, 4) the previous crop, 5) the time of planting, 6) the way the planting is done, 7) the weather conditions, and 8) the neighboring vegetation.

7. The Location and Drainage

a. Information Concerning the Influence of the Location

1. A High Location Effective Against Rust. -- From the earliest times to the present day the devastation caused by rust has been related to the location of the fields, generally in that it is believed that rust does more damage in damp, shady places than elsewhere. Such beliefs can be traced back to ancient times. Thus Theophrastus (371-286 B.C.) mentions in several places (I, Book 8, 10; II, Book 4, 14) that rust affects grain in high, windy places inconsequentially or not at all, while it rages in valleys and wind-protected locations. The same opinion is found in Pliny (I, Ch. 17, § 154) at the beginning of our era (23-79 A.D.).

In agricultural manuals old and new, including that of Arrhenius (I, 61) published in 1888 we encounter the same notion, which is also ... in several writings of ...