INFECTION EXPERIMENTS
WITH
PUCCINIA HELIANTHI SCHW

by

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Great variation exists among the rusts and other fungous parasites with reference to the number of host plants that may be infected by the same morphological species. Some are confined to a single host species, as the marsh elder rust, *Puccinia xanthifoliae*: others range over two or more species of one host genus, as the sunflower rust, *Puccinia helianthi*: while still others range over two or more genera and often on different tribes of the same family, as the grass black stem rust, *Puccinia graminis*. The heteroecious rusts, those that have their aecidial stage on one host and their teleuto-stage on another, may have a particularly wide host range. For example, *Puccinia graminis* has its aecidial stage on various species of Berberis, belonging to the dicotyledons, and its uredo- and teleuto-stage on various grasses, which are monocotyledons. The apple rust has its aecidial stage on the apple and related plants, and its teleuto-stage on the red cedar, a gymnosperm. The autoecious rusts, completing their life cycle on a single host, have a less extensive host range than the heteroecious forms.

As a result of the work of numerous investigators, evidence has accumulated which indicates that, although the fungus occurring on a wide range of hosts has the same morphological characters, it cannot always be transferred from one of its hosts to another. There is evidence of a well marked physiological specialization within the morphological species. For example, the leaf rusts of wheat and rye, Puccinia dispersa, cannot be distinguished from each other under a microscope on the basis of morphological differences; yet the leaf rust of rye cannot ordinarily be transferred by inoculation from rye to wheat and probably is not so transferred in nature. In other words, these two fungi are exactly similar in morphological characteristics but physiologically different.

This phenomenon of physiological specialization has been found in a large number of rusts, powdery mildews and other parasitic fungi by Eriksson, Carleton, Neger, Salmon and others. Various names (Schröter in 1879, "Species sorores"; Klebahn in 1892, "biologische spezies"; Rostrup in 1894 and 1896, "biologiske arten", "biologiske rassen"; Hitchcock and Carleton in 1894, "physiological species"; Eriksson in 1894, "formae speciales") have been given to the groups made on the basis of physiological characteristics. Probably the most expressive term is "Physiological races". Physiological races complicate very greatly the study of the host range of plant parasites; but at the same time they are the basis for the study of disease-resistant varieties of the host species.

The rusts of the grasses have been especially studied by a number of workers in various countries; Eriksson (9) in Sweden, Jaczewski (13) in Russia, Evans (10) in South America, Carleton (7), Stakman (19), Freeman and Johnson (12) in different parts of the United States.

These experiments, carried out in various countries, show that what is apparently the same rust species may consist of a large number of strains or races, which may behave differently in different geographic areas. The following table shows the comparison of the stem rust (Puccinia graminis) groups, "physiological races", in America, Sweden and Russia.

TABLE I. PHYSIOLOGICAL RACES OF PUCCINIA GRAMINIS Pers.

Carleton (in America)	Eriksson (in Sweden)	Jaczewski (in Russia)	Stakman (in America)	Freeman & Johnson (in America)
Puccinia graminis tritici Erikss. and Henn.				
Agropyron richardsoni		Agropyron repens *	Agropyron caninum	
Agropyron tenerum			Agropyron occidentale	
Elymus canadensis			Agropyron tenerum	
Elymus canadensis var. glaucifolius			Bromus tectorum	
Hordeum vulgare			Elymus canadensis	
Hordeum jubatum			Elymus robustus	
Triticum compactum		Festuca gigantea	Elymus virginicus	
Triticum durum		Hordeum vulgare	Hordeum vulgare	Hordeum vulgare

* The form known as Agropyron repens is the Triticum repens of Jaczewski and Eriksson.

TABLE I (cont.) PHYSIOLOGICAL RACES OF PUCCINIA GRAMINIS Pers.

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
		Puccinia graminis tritici Erikss. and Henn.		
Triticum dicoccum			Hordeum jubatum	
Triticum monococcum			Hordeum spartinum	
Triticum spelta		Lolium perenne	Secalis cereale (weakly)	Secalis cereale (weakly)
Triticum turgidum	Triticum vulgare	Triticum vulgare	Triticum vulgare	Triticum vulgare
Triticum vulgare				
		Triticum caninum		

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
		Puccinia graminis avenae Erikss. and Henn.		
Avena fatua	Alopecurus pratensis		Anthoxanthum odoratum	
Avena hookeri	Avena sativa		Avena elatior	
Avena pratensis	Avena elatior		Avena fatua	
Avena sterilis	Avena sterilis		Avena sativa	
Avena sativa patula	Dactylis glomerata	Alopecurus pratensis	Bromus tectorum	
Avena sativa nuda	Milium effusum	Arrhenatherum elatius	Dactylis glomerata	
Avena sativa orientalis	Lamarckia aurea	Avena pubescens	Festuca elatior	
Dactylis glomerata	Trisetum disticho-phyllum	Avena sativa	Elymus canadensis	

TABLE I (cont.) PHYSIOLOGICAL RACES OF PUCCINIA GRAMINIS Pers.

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
Koeleria cristata		Briza media	Holcus lanatus	
Lolium perenne		Bromus arvensis	Hordeum vulgare	Hordeum vulgare
		Festuca ovina	Koeleria cristata	
			Lolium italicum	
			Lolium perenne	
			Phalaris canariensis	

Puccinia graminis secalis Erikss. and Henn.

	Agropyron repens *			
	Bromus secalinus	Bromus inermis	Agropyron caninum	
	Elymus arenarius	Bromus secalinus	Agropyron cristatum	
Hordeum vulgare	Hordeum jubatum	Dactylis glomerata	Agropyron occidentale	
	Hordeum vulgare	Secale cereale	Agropyron repens *	
Secale cereale	Secale cereale	Triticum caninum	Agropyron tenerum	
	Triticum caninum		Bromus tectorum	
	Triticum desertorum	Agropyron repens *	Elymus canadensis	
			Elymus robustus	
			Elymus virginicus	

TABLE I(cont.) PHYSIOLOGICAL RACES OF PUCCINIA GRAMINIS Pers.

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
			Hordeum jubatum	
			Hordeum spartinum	
			Hordeum vulgare	Hordeum vulgare
			Hystrix patula	Triticum vulgare
			Secale cereale	Secale cereale

Puccinia graminis Aperae

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
	Apera spica venti			

Puccinia graminis calamagrostis

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
	Calamagrostis epigeois			

Puccinia graminis airae

Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
Aira caespitosa	Aira caespitosa			

Puccinia graminis agrostis

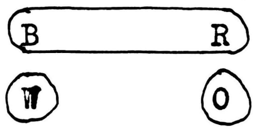
Carleton	Eriksson	Jaczewski	Stakman	Freeman & Johnson
Agrostis canina	Agrostis alba			
Agrostis stotonifera	Aira caespitosa			
Agrostis vulgaris	Apera spica venti			
	Bromus inermis			
	Bromus secalinus			

TABLE I (cont.) PHYSIOLOGICAL RACES OF PUCCINIA GRAMINIS Pers.

Carleton	Eriksson	Kaczewski	Stakman	Freeman & Johnson
		Avena sativa		
		Dactylis glomerata		
		Hordeum vulgare		
		Secale cereale		
		Agropyron repens*		
		Triticum vulgare		
		Puccinia graminis Poae		
	Poa caesia	Poa compressa		
	Poa compressa	Poa pratensis		
		Poa serotina		
		Puccinia graminis Arrhenatheri		
		Arrhenatherum elatius		
		Avena sativa		

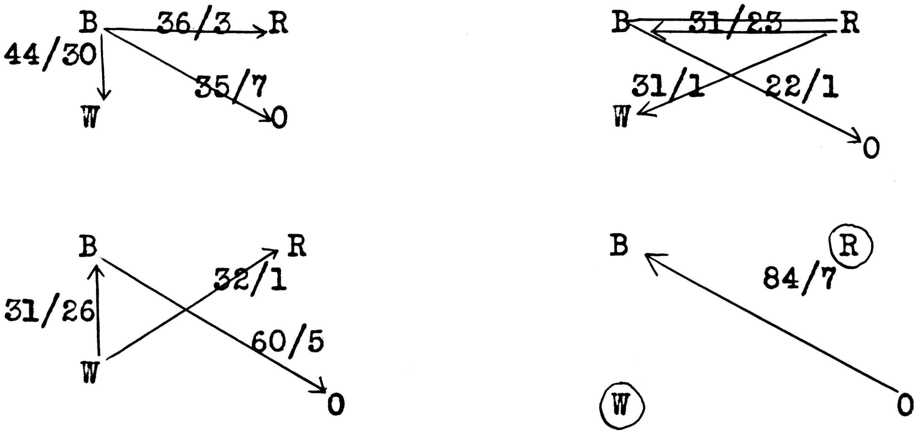
The above data may be summarized briefly by letting W=wheat, B=barley, O=oats, R=rye, and range of infection by extent of circles.

Eriksson (9) in Sweden:



Jaczewski (13) in Russia and Carleton (7) in America:

Freeman and Johnson (12) in America*:



* The upper figure indicates the number of plants inoculated and the lower figure indicates the number infected. Circles show extent of infection: arrows show direction of infection.

Thus it is shown that, in Sweden, the stem rust of wheat, Puccinia graminis tritici, will not infect barley or rye, while the stem rust of barley, Puccinia graminis hordei, and the stem rust of rye, Puccinia graminis secalis, interchange hosts easily. Jaczewski reports that, in Russia, the stem rust of wheat and barley interchange hosts easily, but will not pass to oats or rye; his results agree with those of Carleton.

Stakman and Freeman and Johnson give similar results, but they do not agree with Carleton as to the specialization of Puccinia graminis in the United States. Freeman's results show that uredospores from barley will infect wheat and rye readily, as well as barley and oats to a certain extent; uredospores from wheat will infect rye and barley, but not oats; uredospores from rye will infect rye, wheat, and barley, but not oats; and uredospores from oats will infect oats and barley, but not wheat and rye. The oats can be infected by the rust from both wheat and rye by first infecting the barley with uredospores from these hosts, and then sowing the uredospores produced on the barley in this way on the oats.

There is no sharp limitation of Puccinia graminis on cereals. In other words, the various races are not sharply separated from one another in their uredo-stage. Further investigations should be made, not only with uredospores, but also with other spore forms of this rust.

The stem rust, Puccinia graminis, is heteroecious and belongs to the group with all the spore stages:- spermogonial, aecidial, uredo-, and teleuto-stages. The spermatia, and aecidiospores and teleutospores are produced on the grasses. According to Sydow (22) Puccinia graminis has 18 barberry hosts for aecidiospores and 176 grass hosts for uredospores and teleutospores in Europe, America, Africa, Asia, and Australia. For instance, the stem rust of oats passes its aecidial stage on barberry, while the uredo- and teleuto- stages may be found on practically all species and varieties of oats and on several grasses, some of which are closely related to the oats. If the various races are not sharply separated from one another in their uredo-stage, is it not probable that they are not in their other stages?

Freeman (12) thinks there is a chance in the aecidial stage for the extension of a comprehensive range of a stem rust. On the other hand, Eriksson claims that aecidiospores from a host of one specialized race, will infect only hosts belonging to that particular race. In other words, the aecidial stage on the barberry does not enable the fungus to infect a larger series of host plants, but each form is specialized throughout its entire life cycle.

Additional work has been done along this line by Stakman, Jaczewski, and Arthur. Investigations of Stakman (19) show the following results with the aecidiospores and uredospores of *Puccinia graminis*:

TABLE II. EXPERIMENTS WITH AECIDIOSPORES OF PUCCINIA GRAMINIS Pers.

Host	Aecidiospores of *P. graminis tritici* developed in the field	Aecidiospores from field barberries	Aecidiospores of *Agropyron repens*	Uredospores of *A. repens*	Aecidiospores of wheat	Uredospores of wheat
Barley	57/35	97/66	30/12	27/27	30/24	30/0
Einkorn	60/46	47/14				
Oats	56/1	100/0	29/0	30/0	30/0	46/0
Rye	54/15	80/55	24/12	28/27	30/7	30/6
Wheat,	61/50	95/13	27/26	27/3	30/25	30/30

The upper figure indicates the number inoculated; lower indicates number infected.

These experiments indicate that *Puccinia graminis tritici* and *Puccinia graminis* from *Agropyron repens* do not develop any greater range of infection possibility for cereals after having lived for a time on the barberry. Although these experiments are not extensive, there are indications that physiological races of cereal rusts, at least *Puccinia graminis tritici*, do not lose their specialization tendencies when grown on barberry.

Also, Jaczewski (13) has given his observations on the behavior of aecidiospores from various sources. His results are summarized in Table III.

TABLE III. EXPERIMENTS WITH AECIDIOSPORES OF PUCCINIA GRAMINIS PERS.

Basidio-hosts	Source of Teleutospores: Secale cereale	Triticum vulgare	Avena sativa	Hordeum vulgare	Agropyron repens*	Dactylis glomerata	Bromus secalinus	Lolium perenne	Calamagrostis epigeios	Apera spica venti	Arrhenatherum elatius	Poa compressa	Agrostis alba
Secale cereale	+				+	+	+						
Agropyron repens*	+	+		+	+	+	+	+					
Avena sativa			+										
Hordeum vulgare		+		+	+			+					
Triticum vulgare		+		+	+			+					
Dactylis glomerata	+				+	+	+						
Bromus secalinus	+					+	+						
Lolium perenne		+		+	+			+					
Calamagrostis epigeios									+				
Apera spica venti										+			
Arrhenatherum elatius											+		
Poa compressa												+	
Agrostis alba													+

* Listed as Triticum repens by Jaczewski.

+ = Positive infection

By comparing the above table with Jaczewski's host list for physiological races, Table I., it may be seen that in no instance has the rust been given a wider range by passing through the barberry.

Arthur (6), on the other hand, cites experiments of his own, showing that *Puccinia graminis* has been grown on *Triticum vulgare* from aecidiospores derived from inoculations on *Berberis vulgaris* with teleutospores from *Agropyron repens*, *A. tenerum*, *A. pseudorepens*, *Agrostis alba*, *Cinna arundinacea*, *Elymus canadensis*, and *Sitanion longifolium*, respectively. He concludes that "although in the uredinial stage this rust shows racial strains that inhibit the ready transfer from one species of host to another **** yet in the aecial stage racial strains play no part, and the barberry acts as a bridging host between each and every gramineous host."

In the light of the work of Jaczewski and Stakman it seems that further experimentation on a large number of rusts is necessary before the sweeping statement that "in the aecial stage racial strains play no part" can be accepted.

This same phenomenon of specialization has been described for several other rusts by Eriksson and others. For example, the brown rust of wheat and rye, *Puccinia rubigo-vera* (*P. dispersa* Er. and Henn.), is divided into the following specialized races:

TABLE IV. PHYSIOLOGICAL RACES OF PUCCINIA DISPERSA ERIKSS. AND HENN.

Eriksson (9)	Carleton* (17)	Freeman * (11)
1. Puccinia dispersa secalis		
Secale cereale	Secale cereale	Secale cereale
	Secale montanum	
2. Puccinia dispersa tritici		
Triticum vulgare	Triticum compactum	Hordeum vulgare
	Triticum durum	Triticum vulgare
	Triticum turgidum	Secale cereale
	Triticum vulgare	
3. Puccinia dispersa agropyri		
Agropyron repens**		
4. Puccinia dispersa bromi		
Bromus arvensis		
Bromus brizaeformis		

Ward (23) has further divided the brome rust, Puccinia dispersa bromi, into five physiological races; i.e., Festucoides, Stenobromus, Libertia, Zeobromus (Serrafalcus).

Freeman's results show that Puccinia dispersa tritici will transfer to rye and barley but not to oats. Carleton's results agree with those of Eriksson for the cereals. These are very highly specialized forms and indicate that, in this rust, the physiological races are distinct.

* Carleton and Freeman use the term Puccinia rubigo-vera instead of Puccinia dispersa - Erik. & Henn.
** Triticum repens according to Eriksson.

There are, also, definite specialized races of the crown rust, Puccinia Lolii Niels., (Puccinia Coronifera Kleb.), according to Eriksson (9) and Carleton (7).

TABLE V. PHYSIOLOGICAL RACES OF PUCCINIA LOLII NIELS.

Eriksson	Carleton
1. Puccinia lolii avenae	
Avena sativa	Avena sativa and var. patula, orientalis, nuda
2. Puccinia lolii alopecuri	
Alopecurus nigricans	
Alopecurus pratensis	
3. Puccinia lolii festucae	
Festuca elatior	
4. Puccinia lolii lolii	
Lolium perenne	
5. Puccinia lolii glyceriae	
Glyceria aquatica	
6. Puccinia lolii holci	
Holcus lanatus	
Holcus mollis	

Similar examples of physiological specialization may be found, according to Marchal, Salmon (18) and Reed (15), among the powdery mildews. In Erysiphe graminis, the grass mildew, several well defined physiological races have been demonstrated:

<u>Erysiphe graminis agropyri</u>

Hosts: Agropyron caninum, A. tenerum.

<u>Erysiphe graminis avenae</u>

Hosts: various species of Avena.

<u>Erysiphe graminis bromi</u>

Hosts: species of Bromus

<u>Erysiphe graminis hordei</u>

Hosts: species of Hordeum

<u>Erysiphe graminis poae</u>

Hosts: species of Poa

<u>Erysiphe graminis secalis</u>

Hosts: Secale cereale

<u>Erysiphe graminis tritici</u>

Hosts: Triticum vulgare, T. Spelta, T. durum, T. dicoccum, etc., Hordeum silvaticum*, and various species of Aegilops.

In practically every case the physiological races are restricted to species of a single genus. For example, the conidia from rye infects only rye; conidia from barley infects barley but not wheat, oats or rye. In other words, the mildew on one cereal is unable to pass over onto the species of other cereals.

It is of further interest to note Reed's (15) results with Erysiphe cichoraceaeum DC. It is a very cosmopolitan species, yet it has distinct physiological races which occur on cucurbits, asters, and goldenrods. The form on cucurbits not only occurs on several genera of a single family but passes out beyond

* When young plants were used infection followed; with older plants no infection occurred.

the limits of the family onto *Plantago rugelii* and *Helianthus annuus*. However, it will not transfer to asters and goldenrods. The mildew occurring on these latter hosts in natuer proved unable to infect the squast. Neither the aster mildew nor the cucurbit mildew was able to infect a goldenrod, *Solidago caesia*. Nor was the mildew on this host able to infect asters or squashes.

It is evident from this brief consideration of the specialization in the various groups of fungi, that there are specialized races which are sharply restricted to definite host plants, for example, brown rust o: rye, *Puccinia rubigo-vera secalis*; also, there are cases where there is no sharp limitation to special hosts, but a tendency for a fungus to infect certain plants much more readily than others, for example, the black rust of cereals, *Puccinia graminis*; and cases where the fungus seems able to pass over to a large number of hosts with perfect readiness, as the cucurbit mildew, *Erysiphe cichoracearum*.

Salmon's (17) results on injured plants show that the host plant can be made to vary in its ability to resist the attack of the fungus. He used various means of injury such as the cutting away of the epidermis on one side of the leaf, dipping the leaves into water heated to about 50° C, subjecting leaves to anaesthetics and alcohol for a short time. Conidia from a susceptible plant sown on the injured leaves of the normally immune plant produced infection. The immunity which the host-plant naturally enjoys may be destroyed by injury of one sort or another. There is, however, no evidence of any permanent change in the fungus, for the fungus thus produced is not able to infect the same host in a normal condition.

Stakman (19) used chloroform and ether to determine the effect of an anaesthetic on the resistance of the respective hosts to the stem rusts and obtained the following results:

<u>Puccinia graminis hordei</u>, Barley rust to:

Oats 104/0; 8 slightly flecked

Oats after exposure to ether 40/0; 15 flecked

Oats after exposure to chloroform 39/3; 8 flecked

<u>Puccinia graminis Avenae</u>, Oat rust to:

Wheat 108/1; 5 flecked

Wheat after exposure to ether 90/3; 56 flecked

Wheat after exposure to chloroform 40/0; 19 flecked

Barley 50/0; 10 flecked

Barley after exposure to ether 47/1; 15 flecked

Barley after exposure to chloroform 50/0; 7 flecked

Rye 55/3; 13 flecked

Rye after exposure to ether 64/7; 26 flecked

Rye after exposure to chloroform 46/4; 13 flecked

<u>Puccinia graminis tritici</u>, wheat rust to:

Rye 30/6; 20 flecked

Rye after exposure to ether 50/6; 43 flecked

Oats 46/0; 2 flecked

Oats after exposure to ether 30/0; 10 flecked

Puccinia graminis secalis, Rye rust to:

Oats 50/0; 1 slightly flecked

Oats after exposure to ether 20/0; 2 flecked

Oats after exposure to chloroform 15/0; 5 flecked

Stakman found that anaesthetics aid in breaking down the barriers between races. A high degree of soil fertilization accomplishes the same result. This fact seems due, not to any new ability the rust fungus has of attacking an uncongenial host, but to an increased capacity for development. Thus it may be seen that the use of anaesthetics has some effect in rendering an immune plant slightly more susceptible to the rust. Stakman did not determine the infecting power of the spores obtained, so there is no clue as to whether the fungus is changed.

Therefore, from the above reports, the conclusion may be drawn that changes in the host plant influence the parasitism of a fungus, but make no permanent change in its specialization. And specialization must have come about by variations of the fungus independently of the host. Freeman (12) suggests that rusts widely distributed and subjected to varying conditions are different in their infecting power, thus forming a large number of strains. In this way the difference in the reports of the various investigators is accounted for. Undoubtedly by variation and adaptation to varying conditions a certain rust species widely distributed may form a large number of strains or types, which, when this process has been continued for a considerable time, differ widely in their physiological reactions.

These may become the physiological races.

Ward (24) first suggested the idea that certain plants may serve for the passage of a fungus from one host to another, in cases where the fungus on the one plant cannot directly infect the other. The so-called "bridging species" are supposed to change the infection capacity of a parasite by cultivation on certain hosts. Ward considers *Bromus arduennensis* to be such a "bridging species" for *Puccinia dispersa*, enabling it to pass from brome species of the section Zeobromus (Serrafalcus) to species of the section Libertia. This brome can be readily infected with uredospores from *B. mollis* of the section Serrafalcus, as well as with spores from plants of the section Libertia to which *B. arduennensis* belongs. Spores from these two species on the same hosts gave the following results:

TABLE VI. RESULTS WITH SPORES OF B. ARDUENNENSIS AND B. MOLLIS

Host	Uredospores from B. arduennensis	Uredospores from B. mollis
Libertia		
Bromus arduennensis	7/8	14/13
Bromus arduennensis var. villosus	10/10	1/1
Serrafalcus		
Bromus mollis	8/1	154/119
Bromus secalinus	8/8	61/31

The upper figure represents the number of plants inoculated; the lower figure the number infected.

Although there is a noticeable susceptibility of B. arduennensis to spores from the group Serrafalcus, Ward does not tell us what the behavior of spores thus produced will be, when sown on other plants. The data shows that B. arduennensis is a host for more than one physiological race. It does not enable B. mollis to infect any plant it cannot directly infect. The rust on B. mollis is able to infect directly brome species of four sections, Zeobromus, Stenobromus, Libertia, and Festucoides.

The evidence that Bromus Krausei and B. pendulinus are bridging species is better established. The following data from Ward (24) and Freeman (11) show how these two species may act as a bridge between B. sterilis and B. mollis.

TABLE VII. RESULTS WITH SPORES OF B. STERILIS AND B. MOLLIS

	Ward		Freeman	
Host	Uredospores from B. sterilis	Uredospores from B. mollis	Uredospores from B. sterilis	Uredospores from B. mollis
Serrafalcus				
Bromus Krausei	59/14	27/27	29/14	27/27
Bromus pendulinus	65/17	50/30	53/12	50/30
Bromus molliformus	25/1	6/2	25/1	26/2
Bromus mollis	137/1	154/119	53/1	62/53
Bromus vestitus	4/1	4/3	4/1	4/3
Stenobromus				
Bromus maximus	82/2	74/1	---	---
Bromus Gussoni	60/37	53/6	60/37	53/6
Bromus sterilis	146/126	148/4	48/44	58/0

These are the only species which are infected by spores from both _B_. _sterilis_ and _B_. _mollis_. Of these, three belong to the section Stenobromus and the remainder to the section Serrafalcus.

Ward does not tell what the spores on _Bromus_ _pendulinus_, for example, produced by inoculation with spores from B. mollis, or both of these. Further study with these forms will have to be made to determine to what extent they act as bridges.

Freeman thinks that perhaps the inference may be drawn that intermediate forms exist between _B_. _mollis_ and _B_. _sterilis_. Also, _B_. _Krausei_ is remarkable in the case of infection from both species, and there is probably some other factor to be considered besides the morphological and physiological factors involved in the systematic position, because if _B_. _Krausei_ is an intermediate form, one would not find such extraordinary susceptibility to either species as is actually shown to exist toward _mollis_ spores.

The effect of the wheat rust (_Puccinia_ _graminis_ _tritici_) when barley is taken as a host, is clearly shown by Freeman (12) to be that of enabling a wider range of infection. Direct inoculation gives the following results:

Wheat	Wheat	64/59
	Oats	66/0
	Rye	32/1
	Barley	31/26

Summary of successful inoculations showing succession:

W ⟶ B31/26 ⟶ B 42/28 ⟶ B 16/16 ⟶ R 44/8 ⟶ W 7/7 ⟶ O 50/1.

If Puccinia graminis hordei be transferred directly to other cereals the results are:

B⟶R 36/3⟶B 9/8⟶O 25/5⟶B 9/3⟶W 17/15

The large percentage of infection is probably due to the fact that barley intervenes between rye and oats and between oats and wheat. Puccinia graminis hordei has the widest range of any of the physiological races of the cereal stem rusts.

Already it has been shown that the physiological races of Puccinia graminis are not sharply marked off from each other. The data as reported by Freeman is insufficient to prove that barley is a "bridging species" for the rust on rye and wheat to pass to oats.

On the other hand, Stakman (19) working with the same problem showed that direct transfers have been made from oats to wheat and rye.

TABLE VIII. EXPERIMENTS WITH UREDOSPORES OF PUCCINIA GRAMINIS Pers.

Host	Uredospores from Puccinia graminis hordei	Uredospores from P. graminis avenae	Uredospores from P. graminis secalis	Uredospores from P. graminis tritici
Barley	100/100	50/0, 10 flecked	40/0, 4 flecked	30/30
Oats	104/0, 8 flecked	100/100	50/0, 1 st. flecked	46/0, 2 flecked
Rye	58/26, 29 st. flecked	55/3, 13 flecked	100/100	30/6, 20 flecked
Wheat	100/100	108/1	70/0, 18 flecked	100/100

Upper figure represents number of plants inoculated; lower figure number infected.

Under normal conditions oats show a flecking of the leaves when inoculated with Puccinia graminis tritici, which is much stronger if the plants are first exposed to ether fumes for from 3 to 5 minutes. When aecidiospores produced on the barberry, originating from teleutospores developed on the wheat, are transferred to barley and then oats inoculated with fourth- and fifth- generation uredospores from barley, successful infection took place in one out of 39 attempts, four leaves being distinctly flecked. The success of the inoculation was probably not due to the fact that the rust had passed through the barberry stage. This seems especially true since the other cereals behave in the same way toward the aecidiospores as they do toward corresponding uredospores.

Hybrid plants may play a very important part in the transmission of rust organisms from susceptible to immune varieties. Evans (10) reports some interesting results with Puccinia graminis tritici on wheat hybrids.

TABLE IX. PUCCINIA GRAMINIS TRITICI ON WHEAT HYBRIDS

Host	Wol Koren	Wol Koren x Rust Proof	Wol Koren of (1)	Bobs of (3)	Wol Koren of (2)	Bobs of (4)
Wol Koren	(1) 9/101	(2) 9/833	5/123	5/294	5/971	5/953
Bobs	(3) 9/0	(4) 9/209	5/18	5/63	5/26	5/276

The upper figure indicates the number of plants inoculated; the lower figure the number of pustules.

The rust from the hybrid Wol Koren X Bobs Rust Proof, is not only able to infect successfully the immune parent, Bobs, but also it produces a severer infection on the susceptible parent (Wol Koren) than rust from this parent itself. In other words, a rust which passes through a hybrid plant produces a far more severe infection than the rust from the susceptible parent.

It seems that, in this instance, there has been a change in the infecting capacity of the parasite. The question may be raised whether this change which has been brought about is such that the rust produced on the hybrid would infect a host which would not be infected by uredospores from Wol Koren. Evans gives no results to show the host range for the rust produced on the hybrid. Further work is needed along this line.

Similar examples of "bridging species" have been reported by Salmon (17) and by Steiner (21) in their work with the powdery mildews. Salmon, studying the adaptive parasitism of Erysiphe graminis within the genus Bromus, reports the following:

TABLE X. ADAPTIVE PARASITISM OF ERYSIPHE GRAMINIS BROMI.

Host	Conidia from B. Commutatus	Conidia from B. Racemosus
B. adöensis	36/36	3/1
B. arduennensis	6/6	6/4
B. commutatus	95/95	12/0
B. hordeaceus	9/8	34/34
B. Krausei	4/3	3/3

TABLE X. (cont.) ADAPTIVE PARASITISM OF ERYSIPHE GRAMINIS BROMI.

Host	B. Commutatus	B. Racemosus
B. patulus	7/6	3/3
B. racemosus	36/0	39/39

The upper figure, the number inoculated; lower figure, the number infected.

The mildew of *Bromus racemosus* failed to infect *B. commutatus* while it infected readily *B. hordeaceus*. Furthermore, *B. commutatus* mildew failed to infect *B. racemosus* but infected *B. hordeaceus*. Therefore, Salmon concludes that *B. hordeaceus* may act as a bridge between *B. racemosus* and *B. commutatus*. He tested this in one case by inoculating 22 plants of *B. hordeaceus* with conidia from *B. racemosus*. Twenty plants became infected. The conidia thus produced on *B. hordeaceus* infected *B. commutatus*. Salmon interprets this result as indicating *B. hordeaceus* as a "bridge" for the fungus on *B. racemosus* to pass to *B. commutatus*.

However, Salmon did not determine the infecting capacity of the conidia thus produced on *B. commutatus*. They may have been able to infect both *B. commutatus* and *B. racemosus*, or perhaps only one of these. If only *B. commutatus* should have become infected there would have been evidence that the nature of the fungus had been changed and that ~~that~~ *B. hordeaceus* was a bridging species for *Erysiphe graminis*. The proof as it stands is inadequate, and until the tests are made and positive results obtained *B. hordeaceus* can not be considered a bridging species.

Steiner (21) experimented with *Spaerotheca humuli*. He inoculated with conidia and obtained the following results.

TABLE XI. STEINER'S RESULTS WITH SPAEROTHECA HUMULI

Host	VULGARES Alch. connivens	VULGARES Alch. impexa	VULGARES Alch. pastoralis	PUBESCENS Alch. pubescens
Vulgares Alch. connivens	+	+	+	+
Alch. micans	—	+	+	—
Calicinae Alch. fallax	?	+	+	+
Pubescens Alch. pubescens	—	+	+	+
Alpinae Alch. nitida	—	+	+	—

\+ Positive infection; — negative infection; ? doubtful infec.

Steiner (21) believes that Alch. pastoralis and Alch. impexa are "bridging species" for Spaerotheca humuli. A. pastoralis and A. impexa of the group Vulgares will infect species of four groups. A. pubescens will not infect A. micans but will infect A. connivens, both the latter being of the group Vulgares. Since A. pastoralis and A. impexa will infect both A. connivens and A. micans, they are thought to be "bridging species". For the same reason A. impexa appears as a bridge between A. fallax of the group Calicinae and A. nitida of the group Alpinae. No test experiments were made and data as given does not warrant the assumption.

The best established evidence that a host species may act as a bridge for a fungus to pass to a new host, is given by Ward and Salmon. As has already been shown the experiments were not carried out to determine the change brought about in the fungus by its passage through the "bridging host".

It must be determined what the spores of Puccinia dispersa on Bromus Krausei, for example, produced by inoculation with spores from B. mollis will do on B. sterilis and B. mollis; then, what the spores thus produced will infect. Likewise, with the mildew, Erysiphe graminis, the infecting capacity of the conidia on B. commutatus, derived from inoculating with conidia from B. racemosus passed through B. hordeaceus, must be determined. With the facts thus obtained the degree of change in the fungus in question could be determined. It is only by such series of experiments that a host species may be shown as a "bridging species" for a fungus.

In view of the results obtained by the various investigators with reference to physiological specialization of parasites to particular hosts, the possibility of the host range being extended through changes induced by various external factors, and, further, the question of the possible existence of hosts which may serve as "bridges" to extend the normal range of the physiological races, it is very important that studies bearing on these problems be made on as many forms as possible.

The sunflower rust, Puccinia helianthi, seems a particularly favorable form for carrying out experiments along these lines. Annual sunflowers are easily obtained from seed and grow rapidly under greenhouse conditions. Perennials may be obtained from seed or roots but they do not grow rapidly during their normal resting period. Following inoculation, an abundant supply of uredospores are produced on susceptible species and varieties. The uredo-sori continue to produce spores for ten days to two weeks. Accordingly it is relatively easy to have on hands, at any time, a large supply of viable uredospores for inoculation experiments.

The sunflower rust may be found on leaves, branches, involucral bracts and corolla-leaves of many species of Helianthus. Arthur reports 16 host species. The rust has all the spore forms in its complete life history. The honey-colored spermogonia appear in small clusters. The aecidiospores are orange-red, elipsoid bodies appearing in oblong spots. The uredo-sori are roundish, chestnut-brown, scattered or confluent, often on yellow or pale green spots on the upper surface of the leaf but generally forming a brown mass on the under surface. The uredospores are elliptic or obovate, golden-yellow, and have two germ-pores. The teleutospores, at first intermixed with the uredospores, are chestnut-brown, oblong-eliptical, smooth, and two-celled.

This rust was first observed in South Carolina and Pennsylvania, then it appeared in Russia where the sunflower is largely cultivated, and soon it spread over Europe, extending to Australia.

Aecidia have not been found in Australia, although the rust is plentiful.

Sydow (22) in his Monograph comes to the conclusion that this species possesses no aecidial stage, since he has examined specimens from numerous localities without result, but Carleton (8) has collected the three stages in America and remarks:-----"The aecidium occurs rarely in comparison with the occurrence of other stages, but it is to be found on a number of hosts and occasionally in considerable abundance. This rarity of its occurrence, together with the occurrence of spermogonia so often with the uredo, may be accounted for by the fact that the uredo is often produced by direct teleutosporic infection." Arthur (4) has demonstrated the connection of the aecidial stage with the uredo-and teleuto-stage by sowing teleutospores on leaves and producing aecidia and spermogonia.

Arthur has already obtained some data which indicates that the sunflower rust is divided into physiological races. Table XII gives his results with teleutospores taken from different species of Helianthus.

TABLE XII. PHYSIOLOGICAL RACES OF PUCCINIA HELIANTHI SCHW.

Puccinia helianthi molli	Puccinia helianthi grosse-serrati	Puccinia helianthi laetiflori
Helianthus annuus	Helianthus annuus	Helianthus annuus
Helianthus hirsutus	Helianthus grosse-serratus	Helianthus divaricatus
Helianthus mollis	Helianthus tomentosus	Helianthus Kellermani
Helianthus occidentalis		Helianthus laetiflorus
Helianthus strumosus		Helianthus mollis
Helianthus tomentosus		Helianthus occidentalis
		Helianthus scaberrimus
		Helianthus tomentosus

Arthur interprets the data as indicating the existence of three distinct physiological races. *Helianthus tuberosus* was tested but not infected by teleutospores from either *H. mollis*, *H. grosse-serratus*, or *H. laetiflorus*. Hence it would seem that the form on H. tuberosus is also a physiological race. These results were given from only a few tests. Further investigation may show that *Puccinia helianthi* may be broken up into more races.

According to Table XII, *H. annuus* and *H. tomentosus* are hosts for three physiological races. Thus the question is raised as to whether *H. annuus*, for instance, may serve for the passage of the rust from *H. laetiflorus* to *H. grosse-serratus* or whether it is only a common host for the physiological races.

Arthur (4) reports *Helianthus annuus* as a "bridging species" for the sunflower rust, *Puccinia helianthi*. The following are his results of three year's work.

TABLE XIII. EXPERIMENTS WITH PUCCINIA HELIANTHI SCHW.

Hosts	Source of teleutospores				
	H. mollis 1903	H. mollis 1904	H. grosse-serratus 1902	H. grosse-serratus 1904	H. laetiflorus 1904
H. annuus	++	++	0	+ +	+ +
H. decapetalis	0	0	0	—	0
H. divaricatus	0	0	0	0	+
H. grosse-serratus	0	—	+	+ +	—
H. hirsutus	0	+	0	—	—
H. Kellermani	0	—	0	0	+
H. laetiflorus	0	—	0	—	+ +
H. Maximiliani	—	—	+	—	0
H. mollis	+ +	+ +	0	—	+
H. occidentalis	0	—	0	—	+
H. orgyalis	0	—	0	—	—
H. rigidus	—	0	0	0	0
H. scaberrimus	0	—	0	—	+ +

TABLE XIII cont. EXPERIMENTS WITH PUCCINIA HELIANTHI SCHW.

Hosts	Source of teleutospores				
	H. mollis		H. grosse-serratus		H. laetiflorus
	1903	1904	1902	1904	1904
H. strumosus	—	+	—	—	—
H. tomentosus	+	+	0	+	+
H. tuberosus	—	—	0	—	—

++ Abundant infection: + infection, but slow growth and few or no aecidia formed; — no infection; 0 not sown.

Arthur (4) obtained abundant infection on Helianthus annuus with teleutospores from H. mollis, H. grosse-serratus, and H. laetiflorus. This was the only host which Arthur inoculated that showed this susceptibility. H. tomentosus was infected by spores from the three races, but not so abundantly. Without further experiments he concludes that H. annuus is a "bridging species" for the sunflower rust. His experiments have been too few in number to justify the conclusion, and furthermore, no test experiments were made to prove the statement. Arthur does not report what the rust produced on H. annuus with teleutospores from H. grosse-serratus, for example, will do on H. mollis. He does not tell us what is the result when H. laetiflorus is inoculated with teleutospores from H. annuus that have been infected from H. mollis or H. grosse-serratus. These are a few of the tests which will have to be made before H. annuus can be established as a "bridging species."

Until results of more experiments prove conclusively that H. annuus is a "bridging species" between different hosts for the sunflower rust, it seems best to consider H. annuus as a common host for physiological races of the sunflower rust.

METHODS AND RESULTS

Sunflower seedlings were grown in four or five inch flower pots. The seed was obtained from Henry A. Dreer, of Philadelphia, J. M. Thorburn and Co., of New York, Rev. J. M. Bates, of Red Cloud, Nebraska, E. Bartholemew, of Stockton, Kansas, B. O. Longyear, of Fort Collins, Colorado, and local forms were collected around Columbia, Missouri. When the seedlings had four to six leaves they were inoculated with the uredospores. The uredospores for the first culture were obtained from G. W. Freiberg of the St. Louis Botanical Garden. The teleutospores used were collected on the wild varieties growing in the vicinity of Columbia.

With the exception of experiment three, the plants were inoculated either by rubbing the infected leaf of the stock culture with the thumb and forefinger and then rubbing the leaf to be inoculated, thus distributing spores on both sides of the leaf; or by rubbing or pressing the infected leaves upon the upper side of the leaves to be inoculated. The latter method was the most successful. In experiment three a De Vilbiss Atomizer was used to spray a spore emulsion. The results were not satisfactory, due to the rough pubescent leaves.

After inoculation the pots containing the plants were placed in a saucer of water. A bell-jar was placed over all, supported on wooden blocks to allow an abundant supply of air. The seedlings were kept in this moist chamber twenty-four to forty-eight hours. This was sufficient time for the germination of the uredospores. A longer time proved injurious to the plants.

When teleutospores were used several methods were employed. Teleutospores which had been in a dry room for several months were placed on ice for forty-eight and ninety-six hours before inoculation. Others were placed in cheese-cloth bags and subjected to the varying weather conditions from Febryary 10th to March 3rd. No infection or germination of the spores could be detected either on the plants or in water in Van Tieghan drop cultures kept in moist chambers.

TABLE XIV. SUMMARY OF EXPERIMENTS WITH UREDOSPORES OF PUCCINIA HELIANTHI SCHW.

Hosts	H. annuus	H. annuus var. dwarf double	H. annuus var. Argrophyllus	H. cucumerifolius	H. cucumerifolius var. orion	H. macrophyllus var. giganteus
H. annuus	549/461	36/36			5/5	
" " Western form	31/4 3 fl.	3/3				
" " argrophyllus	56/37	23/23	9/2			
" " double California	19/18	19/19				
" " " chrysantheum	23/18	17/17				
" " " globe flowered	7/7	8/8				
" " " green centered	23/19	9/9				
" " dwarf double	15/13	38/38				
" " " varigated leaved	6/1	1/1				
" " globosue fistulosus	1/1					
" " Henry Wilde	6/5	5/5				
" " primrose colored	20/15	17/17				
" Besseyi	2/ 2 fl.					
" cucumerifolius	32/24	8/8		33/17		
" " diadem	13/6?	26/26				

TABLE XIV. cont. SUMMARY OF EXPERIMENTS WITH UREDOSPORES OF PUCCINIA HELIANTHI SCHW.

Hosts.	H. annuus	H. annuus var. dwarf double	H. annuus var. Argrophyllus	H. cucumerifolius	H. cucumerifolius var. orion	H. macrophyllus var. giganteus
H. cucumerifolius grandiflorus stella	3/2	15/15				
" " hybridus	8/1?	22/22				
" " orion	42/30	21/21			34/32	
" hirsutus *	1/1 fl.	1/0				
" macrophyllus giganteus	37/33	16/16				14/8
" Maximiliani *	24/2 fl.	17/11 fl.				
" Nuttallii	1/0	11/0				
" petiolaris	19/7 fl.	13/6 2 fl.				
" strumosus *	39/0					
" subtuberosus	131/29 fl.	24/14 fl.				
" tuberosus *	19/0	24/11 fl. 2 st.fl.				
" " , French	4/0	3/0				
" " , Jerusalem	10/6 fl.	9/6 fl. 4 st.fl.				

The upper figure represents the number of plants inoculated: the lower figure, the number infected.
fl. flecked
st.fl. strongly flecked
* Hosts reported by Arthur
? data doubtful due to insect injury

The above table is a summary of fifty-seven series of experiments. Eleven host species were inoculated: H. annuus L. and H. cucumerifolius Torr and Gray, (H. debilis Nutt.) and four varieties, H. hirsutus Raf., H. macrophyllus giganteus Willd., H. Maximiliani Schrad., H. Nuttallii Torr and Gray, H. petiolaris Nutt., H. strumosus Willd., H. subtuberosus (var. of giganteus Linn, into which *grosse-serratus* passes); *H. tuberosus* L. (wild, French, and Jerusalem artichokes).

H. hirsutus, *H. Maximiliani*, *H. Nuttallii*, *H. petiolaris*, *H. strumosus*, *H. sub-tuberosus*, and *H. tuberosus* (wild variety) were not infected with uredospores from *H. annuus*; the others were all infected to a greater or less degree. In some cases the results were doubtful, due to injury of the host by insects and fumigation. The amount of infection varied from a few scattered pustules to an almost complete covering of the inoculated leaf. The uredospores were ripe on *H. annuus*, when inoculated from *H. annuus*, in fourteen to seventeen days after inoculation and ready to be used on other plants. If *H. annuus* var. *dwarf double* was the host the spores ripened in eleven days, while only blister-like spots could be seen on *H. annuus* hosts of the same experimental series.

Plants which were infected with uredospores from *H. annuus* var. *dwarf double* had more pustules than when infected with uredospores from *H. annus*. The rust spread to other leaves when kept as a stock culture more readily than did spores from *H. annuus*. The percent of infection, when *dwarf double* was the source of spores, was, in many cases, 100 per cent; and in every instance it was more than when *H. annuus* was the source. With the exception of *French artichoke* the other varieties of *H. tuberosus* was not flecked by *dwarf double*. The wild variety of *H. tuberosus* was not flecked when old plants were inoculated. The Jerusalem artichoke was more strongly flecked with spores of *dwarf double* than with spores of *H. annuus*. Sub-tuberosus was also infected with the rust from *dwarf double* but no pustules were formed. The discolored spots were always roundish and had the same appearance as the spots on a susceptible variety when the epidermis is only slightly raised by the spores.

The uredospores produced on H. annuus var. double chrysanthemum from uredospores of var. dwarf double were sown on var. dwarf double and H. annuus to test their infecting capacity. Six plants of each were inoculated. All the plants were infected. Dwarf double was only slightly infected; there being only a few scattered pustules produced. H. annuus had many pustules on all the inoculated leaves.

Late in September uredospores were collected in the field on H. tuberosus and sown on H. annuus in the greenhouse. Of the eleven plants inoculated two were killed by insects and nine showed good infection. The pustules were distinct and not confluent. They were some darker in color than those produced on H. annuus from other sources. After several days the sori dried in the center leaving a ring of spores about a dead portion of tissue. This rust was kept growing on H. annuus until the fourth-generation uredospores were produced. Twenty-two plants had been inoculated and sixteen infected. The fourth-generation uredospore pustules were nearer together and the infected leaves had more the appearance of the leaves of other stock cultures of H. annuus. The third-generation uredospores were sown on two plants of H. macrophyllus giganteus and produced good infection. The spores thus produced were used to inoculate five plants of H. annuus and five plants of H. macrophyllus giganteus. One small pustule appeared on H. annuus but no infection was produced on H. macrophyllus giganteus.

The tables show that the cultivated variety, _dwarf double_, of _helianthus annuus_ is very susceptible to the rust _Puccinia helianthi_. Further, the rust after passing through var. _dwarf double_ produced 100% infection in cases where pustules were formed. With the exception of French artichokes, all of the varieties of _H. tuberosus_ tested became flecked, indicating infection, but no pustules were formed.

The amount of infection was noticeably greater when uredospores were used from _dwarf double_ than when uredospores were used from _H. annuus_ for inoculation. In passing through _dwarf double_ the virulence of the rust seemed to be changed. The rust could gain entrance into the tissues of _H. tuberosus_ and _H. sub-tuberosus_ to the extent of causing discolored spots but could not produce spores. The range of infection of the rust produced on _dwarf double_ is not much greater than that of rust from _H. annuus_ as is shown by the flecking of the leaves of the Jerusalem artichoke when inoculated with uredospores from _H. annuus_.

SUMMARY

In the experiments eleven species of Helianthus were inoculated with uredospores of *Puccinia helianthi Schw*. taken from *Helianthus annuus*. In addition eleven varieties of *H. annuus*, four varieties of *H. cucumerifolius*, and two varieties of *H. tuberosus* were used.

Full infection, resulting in the production of uredospores, occurred on three species of Helianthus: namely, *H. annuus*, *H. cucumerifolius*, *H. petiolaris* and *H. macrophyllus giganteus*.

All of the eleven varieties of *H. annuus* became fully infected in the various tests.

A slight flecking occurred on *H. Besseyi*, *H. hirsutus*, *H. Maximiliani*, *H. petiolaris* and *H. tuberosus* var. *Jerusalem artichoke*, following inoculation with uredospores from *H. annuus*. Strong flecking on *H. tuberosus* and var. *Jerusalem artichoke*, and a slight flecking of *H. subtuberosus*, *H. petiolaris*, and *H. Maximiliani* followed inoculation with uredospores from *H. annuus* var. *dwarf double*.

The following species failed to give any evidence of infection: *H. Nuttallii*, and *H. strumosus*.

The uredospores collected on *H. tuberosus* in the field infected *H. annuus* and from *H. annuus* passed to *H. macrophyllus giganteus*. Spores from *H. annuus* failed to infect *H. tuberosus* but caused a slight flecking of var. *Jerusalem artichoke*.

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May 22, 1916

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Optical resolution	600 dpi
Color settings	grayscale, 8 bit
File types	tiff

Source information

Format	Book
Content type	Text
Source ID	010-100919669
Notes	Pages typed and single-sided. Title page has signature and perforated property stamp. Some pages have handwritten marginalia and corrections. Letter of approval follows thesis. Many blank pages after thesis.

Derivatives - Access copy

Compression	Tiff compressed with LZW before conversion to pdf
Editing software	Adobe Photoshop CS5
Resolution	600 dpi
Color	Grayscale
File types	pdf
Notes	Grayscale pages cropped, canvassed, and images brightened. Blank pages removed.