IMMUNITY TO FUNGOUS DISEASES AS A PHYSIOLOGICAL TEST IN GENETICS AND SYSTEMATICS, EXEMPLIFIED IN CEREALS.

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CONTENTS.

ONE of the fundamental phenomena in the parasitism of fungi on plants, playing a decisive *rôle* in the selection of immune sorts, is the specialization of parasites. The majority of parasitic fungi are, by their nature, sharply limited in the choice of their hosts, and are attached to definite genera and species of plants. In many cases they are limited to one plant genus. In others, especially in the group of rusts and mildews, there are cases in which the fungus is limited to a few, or even to one host-species only.

In rusts, mildews and a few other families of fungi, the differentiation went so far that the same morphological species are not seldom divided into many independent physiological races, so-called "biologic forms," which are attached to different host-plants. In some instances the various stages of fructification of the same fungus may be differently specialized[1].

The study of the causes of the immunity and susceptibility of plants hitherto has not made much headway; the phenomena of parasitism being too complex, and the drawing up of general statements a matter for the future. But still it has been shown, by the works of Eriksson, as well as by Marshall and his school (17), that immunity depends, not on the anatomical peculiarities of plants, but on the properties of their protoplasmic cell-contents. Salmon and Miss Gibson have also established that positive chemotactic attraction of the germ tubes of fungi by the juice of the host-cells, is not sufficient to produce the normal growth of fungi on the plant. In fact it is now clear to us that immunity depends on very complicated physiological inter-relations between the protoplasm of host-cells and fungus, and that the external differences in regard to immunity to fungal diseases, which are perceptible in various races of plants, are an indication of internal hereditary differences in the constitution of their plasma.

Starting from the nature of immunity, as we understand it at the present day, and from the fact of the specialization of parasites—the connection between the phenomena of immunity and genetics becomes evident. It is obvious that fungi, and, in particular, narrowly specialized ones, may be used in some cases as a physiological test (or,

[1] A very interesting case of this was recently reported by J. Norton for the autoecious rust of asparagus, *Puccinia asparagii* D.C. In regard to the "uredo" or summer stage, some immune sorts of asparagus have been found, but these resistant plants are all susceptible to the same fungus in the "aecidio" stage. (*Methods used in breeding Asparagus for Rust Resistance*, by J. B. Norton. Bureau of Plant Industry, Washington. Bul. No. 263, 1913, pp. 23—24.)

strictly speaking, reagent) for the recognition of the species and races in systematic and genetic studies of plants.

The general idea of a connection between immunity and genetics is certainly very conspicuous, and there are many data to prove it. It is enough to mention the well-known fact that nearly allied species of animals are very often susceptible to the same diseases; nearly related genera of plants very often suffer from the same insects. Several genera of parasitic fungi are exclusively connected with definite families of plants, as for example *Phragmidium* with the family *Rosaceae*.

The general indications of the possibility of applying fungal reactions of plants in ascertaining their affinity, may be found in mycological literature. But, notwithstanding the certainty of a relation between immunity and genetics, very few cases are known of the actual use of fungi or other parasites as tests in genetic and systematic work. There are probably two reasons which explain the neglecting of this method: firstly, because in the majority of cases, fungi are not sufficiently specialized to be employed for the delicate differentiation of nearly related plants, and secondly, on account of the usual divergence of the work of pathologists, genetists and systematists.

As to examples in literature of the use of parasites as physiological tests, I can cite very few. First, Prof. Klebahn in his monograph on rusts (7), pp. 140—141, in the paragraph entitled: "Verwendung der Spezialisierung des Schmarotzers zur Unterscheidung der Arten und Wirte," mentions a case in which by the aid of narrowly specialized rust *Melampsora ribesii purpureae* he found a mistake in the denomination of a willow plant in his garden. A second example occurs in the work of Eriksson entitled: *Ein parasitischer Pilz als Index der inneren Natur eines Pflanzenbastards* (4). In this work he has shown that the hybrid of wheat and rye is immune to brown rye-rust *Puccinia dispersa* and susceptible to brown wheat-rust *P. triticina*, which proves that this plant is nearer to wheat than to rye (16, p. 104). A third case is furnished by E. M. Vasiliev's observations on the injurious insects of maize in which he makes an attempt to connect the number of species of these insects with the origin of this plant (15)[1].

[1] In Darwin's *Variations of Animals and Plants under Domestication*, second edition, Vol. II, Chap. XVIII, we find the following footnote about the affinity of *Aperea* and guinea-pigs. "I sent to Mr H. Denny, of Leeds, the lice which I collected from the wild *Aperea* in La Plata, and he informs me that they belong to a genus distinct from those found on the guinea-pig. This is important evidence that the *Aperea* is not the parent of the guinea-pig; and is worth giving, as some authors erroneously suppose that the guinea-pig since being domesticated has become sterile when crossed with the *Aperea*."

Working both on the immunity and systematics of cereals, I often had an opportunity of proving the connection between the relationship and fungal reactions of these plants. My observations led me to the conclusion that fungi, as a physiological test, may be very useful in the genetic and systematic study of this plant group.

Some of the results obtained have been published (16). Here I propose to cite several general conclusions from work done, and then add new data.

To begin with, a few words about the application of fungal tests for the purposes of the systematics of cereals. At the present time attention, in the systematic study of these plants, is being directed towards numerous small constant botanical units, the so-called "races." The principal justification of this work is a very real need for the drawing up of a detailed catalogue of cereal races, useful alike to the worker in genetics and to the practical agriculturist. In the description of these races not only morphological characters are taken into account, as is usual in purely systematic studies, but also physiological ones.

The extremely narrow specialization of many fungi found on cereals, and the well-known fact of the existence of differences in the degree of susceptibility to diseases amongst various sorts of them, warranted first of all the attempt to use fungal tests for the recognition of the races.

In fact, by the aid of this method, I was easily able to divide many varieties[1] of wheat and oats into races. The important *rôle* in the systematic study of such a character as the degree of immunity is increased, as practice in its application has shown, by the circumstance that the physiological individualisation of race is very often accompanied by morphological characters which, however, are externally not very conspicuous. In these cases the peculiarity in behaviour towards fungi obliges the observer to pay more attention to this or that previously unsuspected race, and in the end he usually succeeds in finding in it some other confirmatory differences[2].

[1] We use here the word "variety" in a purely botanical sense. (See F. Koernicke, *Handbuch der Getreide*, 1885.) In the group of cereals "varieties" usually are collective notions, and some of them include many independent morphological and physiological forms—"races"—the smallest systematic units.

[2] Parenthetically we must remark that the definition of degree of susceptibility to a certain disease is not quite simple. In fact, the exactitude of many old works in this respect is so small that in our days we are obliged to obtain these data anew. More details about the definition of degree of immunity are given in our paper (16), Chapter I.

With respect to wheat the application of fungal reactions is a specially grateful method, because in this instance we have at our disposal many narrowly specialized parasites, in other words many sensitive physiological reagents, as brown and yellow rusts, mildew, etc. When one test is not sensitive enough to distinguish our races, we may have recourse to a second, a third, and so on.

In the above-mentioned paper (16) many examples of such a division of varieties of oats and wheat into races are given. As a, perhaps, interesting result, I may mention that many races were found to exist in some of the less common varieties, as *Avena diffusa* As. and Gr. var. *brunnea* Kcke., var. *cinerea* Kcke., var. *montana* Al., and in several rare varieties of *Triticum vulgare* Vill.

In the species *Triticum dicoccum*, which is represented by many varieties and races, it was ascertained that there exist two groups of races: one immune to brown rust, the other susceptible to it. The genetic significance of this will be dealt with later on. Here we must observe only, that the resistant forms of *Tr. dicoccum*, which were in our collection, are morphologically, in the structure of ears and leaves, very like several varieties of *Tr. durum*. The degree of immunity of these latter to brown rust is also nearly the same as in the resistant races of *Tr. dicoccum*.

The most interesting example of the application of this method to the systematic study of wheat I met with, is the following:

In the investigation of 580 sorts belonging to the species *Tr. vulgare*, which in general is very susceptible to mildew (*Erysiphe graminis* D.C.) and to different rusts, we found to our surprise a spring race which was perfectly immune to mildew. Notwithstanding many attempts at artificial infection in the field, in the greenhouse or under bell-jars, this race remained quite immune. Not one pustule of mildew was found on this wheat, whereas other races of *Tr. vulgare* in these conditions were severely attacked by the above fungus. This wheat proved also to be relatively very immune to brown rust (*P. triticina*). The seeds of this wheat were obtained from a German seed merchant under the name of "Persian Wheat."

Such an extraordinary immunity as distinguished this race from other races of *Tr. vulgare* and from the majority of races belonging to other species made me pay exceptional attention to this form, and the preliminary investigations so far made have revealed many further peculiarities in it. Although a number of morphological characters show that it belongs to common wheat, namely to *Tr. vulgare* var.

fuliginosum Al.[1]—a variety with black bearded hairy ears and red grains—yet this form is distinguished by many other characters from all our races of *Tr. vulgare,* which are not included in the classification of Koernicke.

The straw of this wheat is relatively full of pith. Usually, the varieties of *Tr. vulgare* have a hollow straw. The stem-knots of this wheat are visibly hairy; generally they are smooth in the species *Tr. vulgare*. The rachis of "Persian Wheat" is only half as broad as in common wheats. Ordinarily in wheat, only flowering glumes possess an awn. In this "Persian Wheat," the empty glumes are also awned[2]. Besides these, there are other small morphological differences in the structure of ear and leaf.

By crossing this wheat with other varieties of *Tr. vulgare,* it was observed that the percentage of successful results was very small. The same fact was repeated the next year. Usually in the same conditions the percentage of success in our crossings of different varieties of *Tr. vulgare* was very high. In the F_1 hybrids (♀ "Persian Wheat" × ♂ *Tr. vulgare* var. *lutescens* Kcke.) about 70 % of the spikelets were sterile.

Finally in some of our crossings of susceptible races of wheat with immune ones, the susceptibility to mildew was clearly dominant, and F_1 hybrids were severely attacked by this fungus, as was seen in the experiments of Prof. Biffen with barley. But in the case of crossing "Persian Wheat" with a very susceptible race (*Tr. vulgare* var. *lutescens* Kcke.), only after many efforts did we succeed in infecting slightly the F_1 hybrids, when in the same conditions the susceptible parent was severely attacked. In other words immunity in this instance is not "recessive."

Without dwelling further on this case, we must remark only that all that has just been said about this wheat allows a systematist to separate it from other varieties of *Tr. vulgare,* and makes it of special interest for the genetist.

An instance I came across in the investigation of barley is analogous to that described by Prof. Klebahn with willows. In our collection we had some samples of naked two-rowed barley from different parts of Russia. In the classification of Koernicke (1885), which we made use

[1] The name *Tr. vulgare* var. *fuliginosum* Al. is a collective name. We know quite ordinary susceptible wheats of the species *Tr. vulgare* which have black, hairy, bearded ears with red grains, like "Persian Wheat," and which must be placed in Koernicke's classification under the name "var. *fuliginosum.*"

[2] This character is observable also in a few races of *Tr. vulgare,* belonging to different varieties, which are cultivated in Asiatic Russia and Persia.

of for the identification of barleys, all naked two-rowed barleys are represented by one variety—*Hordeum distichum* var. *nudum* L. To this variety we had referred, after identifying, all our naked two-rowed sorts of barley. But from observation of these barleys during two years, it was noticed that one of these parts (a pure line) was noticeably less susceptible to *Puccinia simplex* Eriks. than others, although growing side by side. This circumstance obliged me to pay more attention to the form in question, and in the result it was found that we had a very rare variety, which was wanting in the old classification of Koernicke. It is distinguished from var. *nudum* L. by weak development of the lateral spikelets (as in var. *deficiens* Steud.), and it was described only in the posthumous article of Koernicke (8), published in 1908, under the name of *Hordeum distichum* var. *nudideficiens* Kcke. We received this variety from Caucasus (Daghestan).

I now append some examples of the connection of the fungal reaction of cereals with their genetics.

Characteristics of the Eight Species of Wheat in relation to Rust and Mildew.

After the work of Prof. Biffen and Nilsson-Ehle, which proved that immunity and susceptibility to fungal diseases is subject to the Mendelian rules of inheritance, it would seem very natural to suppose that the distribution of these characters amongst hundreds of varieties and races of cereals is quite accidental and without any definite order, as immunity and susceptibility may be combined by the aid of crossing with any group of morphological characters. Especially it would be natural to suppose it to be so in such a group as wheats, seven species of which (*T. vulgare, T. compactum, T. durum, T. polonicum, T. turgidum, T. Spelta* and *T. dicoccum*) have been proved to be fertile by crossing[1].

In reality, it is far from being so.

After investigation of about 800 sorts (represented by pure lines) of spring and winter wheat, collected from different parts of Europe and Asia, with regard to fungi prevalent in European Russia (*Puccinia triticina* Eriks. and *Erysiphe graminis* D.C.), and after classifying the sorts and tabulating these data, we came to the conclusion that in general each of the eight species of wheat, including dozens of varieties and races, has a definite characteristic behaviour in relation to fungi (16, pp. 29—54, 94—102).

[1] See works of Vilmorin, Beijerinck, Rimpau, Tschermak, Biffen and others.

For example, all the cultivated varieties of *T. durum* and *T. turgidum* are relatively immune to brown rust. All known wild and cultivated varieties of *T. monococcum* are perfectly immune to brown rust.

Many scattered data, which were found in old and recent literature, referring to the same or other varieties, prove the correctness of this conclusion (the literature is given in the above-mentioned paper 16, pp. 94—99, 5—6) and allow us even to apply, in some degree, this generalisation to the relation of the species of wheat to other fungi, as yellow rust *P. glumarum.* For instance, all varieties of *T. monococcum*, in accordance with published data, are perfectly immune to yellow rust. The different varieties of *T. durum* and *turgidum* are relatively immune to the same rust.

In general, the characteristics of the eight species of wheat in relation to the fungi by which they are attacked in Russia are as follows:

In relation to *Puccinia triticina* Eriks.[1]

susceptible	*resistant*
Tr. vulgare Vill. (there are a few immune races)	*Tr. durum* Desf.
Tr. compactum Host.	*Tr. polonicum* L.
Tr. Spelta L.	*Tr. turgidum* L.

perfectly immune

Tr. monococcum L.

Tr. dicoccum Schr. has both susceptible and immune races.

In relation to *Erysiphe graminis* D.C.

susceptible	*resistant*
Tr. vulgare Vill. (with the exception of a few races)	*Tr. durum* Desf.
Tr. compactum Host.[2]	*Tr. polonicum* L.
Tr. Spelta (a little less than the preceding ones).	*Tr. turgidum* L.
	Tr. monococcum L.

Tr. dicoccum Schr. has both susceptible and immune races[3].

[1] In the paper (16) are given the coloured plates, illustrating the differences in susceptibility of wheats and oats to brown, black and crown rusts.

[2] Only one race, belonging to the variety *Tr. compactum* var. *creticum* Mazz. proved to be relatively resistant to mildew. (The same was observed in America by Prof. Reed.)

[3] These characteristics of species are based on observations in fields under different conditions of manure, soil and climate. In greenhouses brown and yellow rusts do not develop to any considerable extent even by artificial infection; on the contrary, the

Only in *Tr. vulgare* and partly in *Tr. compactum* there are a few relatively immune races—exceptions to the general characteristic of these species, as susceptible to brown rust and mildew. One of the extreme exceptions is the above-mentioned "Persian Wheat"; several of the other more or less immune races, without any doubt, represent products of artificial crossing in recent times (16, p. 96).

Also, briefly speaking, in the group of wheats we meet with a case of specific peculiarities of whole species in their fungal reactions, notwithstanding the great polymorphism of these species.

The genetic significance of these data I shall shortly touch upon. The practical importance of this generalization for the selection of immune sorts is evident, for it simplifies considerably the work of the plant-breeder.

Characteristics of the Species of Oats in relation to Rusts.

As in Russia, so in England and other countries, oats are attacked very severely by two species of rust: crown or leaf rust *P. coronifera* Kleb., and black or stem rust *P. graminis* Pers.

Observations in Moscow showed that the majority of cultivated and wild oats are very susceptible to crown rust.

Of 323 sorts of *Avena sativa* L. (*A. diffusa* Aschr. and Gr., and *A. orientalis* Schreb.) examined, 297 belonging to the majority of known botanical varieties of cultivated oats (8) proved to be very susceptible; 21 less susceptible, and 5 races (belonging to the varieties var. *cinerea* Kcke., var. *brunnea* Kcke., and var. *grisea* Kcke.) proved to be relatively very immune to crown rust. The great majority of these

conditions of greenhouses are very favourable to mildew of cereals; the fungus in the conidial stage lives, for example, in greenhouses much longer than in the open air, and in general the plants are always more attacked by mildew in greenhouses than in fields. And even more or less resistant races of wheat, for instance different representatives of *Tr. durum*, *polonicum*, may be severely attacked in the greenhouse, as also under the bell-jar, by *Erysiphe graminis*. Immune races do not "lose" their immunity in greenhouses. The difference in susceptibility may be observed during the first days of infection, but the fungus develops better under these conditions. The most important fact is that even under these conditions such races as "Persian Wheat" or several races of *Tr. dicoccum* remain uninfected.

By what is said above is removed the controversy relating to the characteristics of *Tr. durum* and *Tr. polonicum* in our work and that of Prof. Reed in America (*Phytopathology*, Vol. II, No. 2, 1912), who defined the degree of susceptibility of 78 sorts of wheat by the aid of artificial infection of seedlings under bell-jars. The data of the characteristics of other species of wheat, in Russia and America, in general coincide.

last 26 races belong to varieties with black and grey grains (flowering glumes), and in general they are morphologically different from susceptible races (16, pp. 15—18, 94—95).

The various examined races of wild oats, belonging to the species *A. fatua* L., *A. Ludoviciana* Dur., and *A. sterilis* L., all proved to be very susceptible to crown rust.

Avena brevis Roth., *A. strigosa* Schreb., and *A. nuda* L. var. *biaristata* Aschr. and Gr. are relatively immune to this rust.

A different result was obtained with *black rust.* Of 350 examined sorts of cultivated and wild oats, belonging to nearly all known botanical varieties, *only two races* of the species *A. sativa* L. proved to be relatively immune. One of them (more resistant) belongs to the var. *brunnea* Kcke., the other (less resistant) to the var. *montana* Al., two varieties with dark flowering glumes, and both these races are morphologically very different from the other susceptible races of the same varieties; for instance, they are very low plants and are characterized by very thin straw; practically both are of small value. *All other cultivated and wild varieties belonging to six species are badly attacked by P. graminis.*

In other words, as a result of these observations, we come to a simple statistical conclusion as to the very slight probability of plant-breeders' finding oats resistant to black rust.

This conclusion will be quite logical if we remember that black rust of oats is a very weakly specialized fungus, which lives freely not only on the genus *Avena*, but also on *Alopecurus, Millium, Bromus, Lamarckiana, Phalaris, Koeleria, Festuca* and other genera of *Gramineae.* For genetists it is quite natural to conclude that if the fungus does not distinguish generic differences, there is very little probability that it will sharply distinguish racial differences in the species *A. sativa* L.[1]

[1] A similar argument may be applied to the ergot of cereals—*Claviceps purpurea* Tul. The same biologic race of this fungus, according to Stäger's experiments, lives on rye, barley, wheat, *Anthoxanthum, Hierochloa, Arrhenatherum, Dactylis, Poa, Briza* and other genera of *Gramineae.* Theoretically, therefore, there is very slight probability for plant-breeders to find a great difference among races of rye, barley and wheat in their susceptibility to this fungus. The great difference between rye, barley and wheat in the degree of infection by ergot (the two latter are very rarely attacked by ergot), is evidently connected with the different modes of flowering of these cereals. Rye usually flowers with opened glumes, wheat and barley with closed glumes; and the closed mode of flowering prevents the two latter from being infected by ergot. Eventually all the

Fungal Reactions of Species of Wheat and their Genetic Relationships.

Now turning again to the general characteristics of the species of wheat and oats in relation to narrowly specialized fungi, we shall see that they have not only significance for plant-breeders, but deserve serious attention on the part of students of genetics. As is known, the genetic relations of cereals are far from being solved. Every new criterion for the understanding of this problem is useful and valuable. It is especially so because the usual criterion of degree of affinity—sterility or *vice versa*—fertility of hybrids cannot always be used in the group of cereals. For instance, the seven species of wheat are so nearly allied that they give fertile hybrids. To understand the genealogy of this group, botanically restricted but nevertheless represented by an immense number of independent forms, we must employ finer methods.

On looking into the characteristics of eight species of wheat in relation to rusts and mildew, we cannot help being struck by their complete agreement with several genetic conceptions which are more or less established concerning their relationship.

eight species of wheat, according to our observations in Russia, may be slightly attacked by ergot, especially when wheats are cultivated side by side with rye.

In his second paper on "Studies in the Inheritance of Disease-resistance," *Journ. of Agr. Sc.*, Vol. IV, Part 4, 1912, Prof. Biffen communicates a curious fact of the occurrence in the F_2 hybrids of Rivet (*Tr. turgidum* L.) with several varieties of *Tr. vulgare* of some plants which were attacked by ergot, although the parent forms had never been seen to be attacked by this fungus. Prof. Biffen explains this fact, as a result of combination of two Mendelian factors of susceptibility to ergot, which are separated in their parents, and in separate form cannot produce the susceptibility of wheat to ergot.

The apparent contradiction of this case of distinct difference in susceptibility to ergot of wheat plants to the above-mentioned general statement, however, is easily removed by a simpler and more probable interpretation of this fact, than that given by Prof. Biffen.

Already in 1891 Prof. Rimpau, in his *Kreuzungsprodukte landwirtschaftlicher Kulturpflanzen*, pp. 11—12, had noticed the fact that in the same crossing of Rivet and *Tr. vulgare* there appear in F_2 hybrids *some sterile plants*. The sterile plants of cereals as is known flower usually with open glumes, remain many days in this state, and commonly are badly attacked by ergot. (See E. Tschermak, "Die Blüh- und Fruchtbarkeitsverhältnisse bei Roggen und Gerste und das Auftreten von Mutterkorn," *Fühlings landwirtschaft. Zeitung*, LX. 1906.) The sterile plants of F_1 of the hybrid of wheat and rye, for example, are severely ergotized.

Evidently the same fact of appearance of sterile plants was observed in the experiments of Prof. Biffen at Cambridge, and, as might be supposed, *these sterile plants* were attacked by ergot.

(*a*) *Tr. monococcum* L. is unanimously separated by genetists as an independent species from all the other seven, principally on account of the sterility of its hybrids with the other seven species of wheat, which has been proved by many investigators [Vilmorin, Beijerinck, Koernicke, Tschermak] (18), whereas all these latter (*Tr. vulgare, compactum, dicoccum, turgidum, durum, polonicum,* and *Spelta*) in crossing give more or less fertile hybrids[1]. The wild progenitors of our cultivated varieties of *Tr. monococcum* have been known for a very long time, whereas the wild prototypes of other species were found only a few years ago.

The genetic individualisation of *Tr. monococcum* is confirmed too by its fungal reactions. All its known wild and cultivated varieties are perfectly immune to brown and yellow rusts, and in this respect occupy a separate place among other species of wheat. In literature we find also indications that they are equally immune to stinking smut, *Tilletia tritici* (6).

(*b*) *Tr. compactum* Host.—dwarf wheats, according to modern views are so nearly allied to common wheats, *Tr. vulgare* Vill., that many authors unite them into one species. As we see in the table given above, their fungal reactions on mildew and brown rust are the same.

(*c*) *Tr. polonicum* L. and *Tr. turgidum* L. by systematists and genetists (Koernicke, Schulz, Beijerinck and others) are considered as species nearly allied to *Tr. durum* Desf. "Bei einzelnen Formen" (of *Tr. turgidum*)—says Schulz—"kann man zweifeln, ob man sie zu *Tr. turgidum* oder *Tr. durum* zurechnen soll" (10, p. 150). "*Tr. polonicum*" —says Beijerinck—"ist ohne Zweifel nur eine halbmonströse Abart von *Tr. durum*" (3). "Es giebt unter *Tr. durum*"—says F. Koernicke— "Sorten, deren Körner in der Länge, Gläsigkeit und der hellen Farbe genau denen von *Tr. polonicum* gleichen" (8, p. 397). These three species are alike not only in the structure of their ears, but also in their vegetative organs.

The characteristics of these species in their fungal reactions to *P. triticina*, *P. glumarum* and *Erysiphe graminis* are identical.

(*d*) *Tr. dicoccum* Schr.—Emmer—according to the current view, is a polymorphic progenitor species from which the susceptible and

[1] Only quite recently M. Blaringhem reported in *C. R. de l'Acad. des Scienc.*, 1914, T. 158, No. 5, that he succeeded in obtaining a few fertile hybrids ♀ *Tr. monococcum* L. var. *vulgare* Kcke. × ♂ *Tr. durum* var. *Macaroni*, as a result of many crossings of these species. Many of his other crossings of *Tr. monococcum* with different species, proved to be unsuccessful or sterile.

immune species as *Tr. vulgare*, *Tr. durum* and others (except *Tr. monococcum*) are descended. This view, as is known, has been confirmed in our days by the finding of numerous forms of wild *Tr. dicoccoides* in Palestine and Syria by A. Aaronsohn, and in Persia by Strauss. In accordance with this view we find in the species *Tr. dicoccum*, races both immune and susceptible to mildew and brown rust.

The susceptibility to brown wheat rust and mildew of some races of wild *Tr. dicoccoides*, which were kindly sent to me by Mr A. Aaronsohn and were examined in Moscow in their relation to fungi, once more confirmed their near relationship to cultivated wheats. Prof. Tschermak and A. Aaronsohn proved also that *Tr. dicoccoides* gives fertile hybrids with cultivated wheats (14).

Fungal Reactions of Species of Oats and their Genetic Relationships.

The same parallelism of fungal reactions and the genetic relations of plants is observable in oats. According to the present views which are based on systematic study and experiments in the crossing of wild with cultivated forms, oats have a *polyphyletic* origin. According to recent work by Dr Trabut in Algeria (13), Dr Thellung in Switzerland (12) and A. F. Malzev in Russia, we regard *A. fatua* L., *A. sterilis* L. and *A. Ludoviciana* Dur. as the ancestors of our cultivated forms *A. sativa* L. (*A. diffusa* Asch. and Gr., and *A. orientalis* Schreb.)[1].

As was said before, the representatives of all these species examined in Moscow proved to be equally susceptible to the narrowly specialized crown rust *P. coronifera*, like the majority of cultivated oats.

A. strigosa Schreb. and *A. brevis* Roth., two rarely cultivated species, which are morphologically much alike, and which by our crossing in Moscow proved to give fertile hybrids[2], are relatively immune to crown rust. In this respect, they are distinguished from the above-mentioned wild and cultivated oats.

Many attempts at crossing of *A. strigosa* (two varieties) with cultivated *A. sativa* (*A. diffusa* Asch. and Gr.) repeated during two years in the Moscow Agricultural Institute proved to be unsuccessful, whereas under the same conditions the crossing of *A. fatua* and *A. sativa* was

[1] The origin of naked cultivated oats, represented by very different morphological forms hitherto, is far from being clear.

[2] This crossing was done after their similar reaction on fungi was known to us, and in this case the similarity in fungal reaction suggested the possibility of crossing these two species.

successful and the hybrids were fertile. This fact confirms the peculiar genetic place of *A. strigosa* amongst other cultivated oats, which was suggested by its fungal reaction.

Finally, the isolated genetic position of *A. strigosa* is proved by the fact, which we find recorded (11), that it is also immune to smut *Ustilago avenae*, whereas the cultivated forms of *A. sativa* are usually severely attacked by this fungus[1].

Some other examples might be given illustrating how, by the aid of genetic knowledge, the differences of various cereals in their behaviour to fungi become clearer; and *vice versa* how fungal reaction helps us to understand the genetic relation of plant forms. But the complete enumeration of all these examples would be out of place in this paper.

One objection may be raised against the broad application of fungal reaction for genetic purposes.

This is the phenomenon of so-called "bridging species"—cases in which the biologic form of a fungus, after living on certain of its host-species ("bridges"), becomes capable of infecting a species, which it cannot infect after living on its other host-species. Pole Evans also showed with black rust of wheat *P. graminis*, that very susceptible F_1 hybrids of immune and susceptible varieties may serve as a "bridge" between susceptible and immune sorts.

But against this, in the first place, there are only very few cases known of existence of "bridging species[2]." In the case of fungi of cereals, they are found only in *Puccinia graminis forma* sp. *tritici* and not in *P. glumarum*, *P. triticina*, *P. simplex* (2, 5). Furthermore, we must not forget that the biologic forms of *P. graminis* are relatively weakly specialized fungi; for example, *forma* sp. *tritici*, as has been shown in different countries, can infect not only wheat but, more or less, barley also[3].

[1] Morphologically *A. strigosa* is very like *A. barbata* Pott.; and Dr Trabut and Thellung account the latter as the progenitor form of the former species. It would be very interesting, therefore, to know the fungal reaction of *A. barbata*.

[2] "Bridging species" are found in *P. Symphyti Bromorum* F. Müll. (M. Ward and Freeman), *Erysiphe graminis* D.C., living on *Bromus* (E. Salmon), in *P. graminis forma* sp. *tritici* (Freeman and Johnson), and *Sphaerotheca Humuli* on *Alchemilla* (Steiner).

[3] One of the conclusions to which Freeman and Johnson came after their numerous experiments with biologic forms of *P. graminis* is that "two biologic forms may inhabit the same cereal without being identical" (5, p. 75). This statement, as also the fact, well-known to mycologists, of the existence in Australia of a different race of *P. graminis f. tritici*, which cannot infect *Berberis*, and all that is known about the difference in

Secondly, as has already been remarked by Prof. Biffen (2, pp. 428—429), two facts speak against the great *rôle* of "bridging species": first, the fact that immune varieties may be grown dozens of years in close proximity to susceptible ones, severely attacked by fungi, and still remain quite resistant; the second fact is the possibility of obtaining immune races by crossing.

Finally, it may well be conceded that the exactitude of fungal reactions must be studied before using them for genetic purposes, as with reactives in chemistry. With fungi of cereals, this preliminary work is happily already more advanced than it is with any other group of fungi[1].

In conclusion, we need only remark that the degree of sensitiveness of fungal reaction, for instance, with cereals up to the present time is not exceeded by that of the so-called "serum" methods, applied to plants. It is hardly necessary to add that fungal reaction technically is much simpler than the "serum" method in its application for the recognition of individuals.

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Note. While this paper was being printed there appeared in the *Zeitschrift für Pflanzenzüchtung*, April 1914, Bd. II, Heft 2, a very interesting paper by Dr Zade entitled: "Serologische Studien an Leguminosen and Gramineen." In his investigation with cereals, using the "serum" reactions as a chemical test for the genetics of these plants, Dr Zade, as we understand his tables, comes to quite the same conclusions concerning the genetic relationship of oats and wheats, to which we came using fungal tests for the same purpose.

So, the tables of experiments on different species of *Avena* show that the *A. fatua* gave almost the same reaction as *A. sativa.*

A. strigosa, which according to our investigation is genetically more distant from *A. sativa* than *A. fatua*, gave in the experiments of Dr Zade, when he used the weak "serum" solution of *A. sativa*, a much weaker reaction than *A. fatua*.

specialization of this fungus in different countries, suggest the suspicion that it is possible, in the same biologic form, more than one race of fungus may exist, and these races differ more or less in their specialization. And, perhaps, in some instances the same phenomenon of "bridging species" is the result of unconscious selection of different races of fungi by the aid of different hosts. Certainly this question can be solved only by means of pure cultures of fungi.

[1] For the purpose of greater exactness, the conditions of the use of fungal reactions must be borne in mind too, because, like chemical reactions, they change under differing conditions; although in general the *rôle* of external conditions (climate, soil, manure, etc.) in changing immunity is very often too exaggerated in mycological literature (16, pp. 99—102).

The similarity in the case of wheats is even more striking. So, *Tr. monococcum*, according to Dr Zade's experiments, occupies a separate place. Three species *Tr. durum*, *Tr. polonicum* and *Tr. turgidum*, which have the same fungal reactions, had the same "serum" reaction. The *Tr. vulgare*, *Tr. compactum* and *Tr. Spelta*, both in relation to fungi and in their "serum" reaction are very similar.

The similarity of "serum" reaction of *Tr. dicoccum* with that of *Tr. durum*, *polonicum* and *turgidum* again does not contradict our results; for probably Dr Zade used for his experiments a variety of *Tr. dicoccum* which is immune to brown rust. It is to be regretted that Dr Zade does not give the names of the varieties with which he worked. This makes a complete comparison of results difficult.

On account of the great polymorphism of the species *Tr. dicoccum* (and *Tr. dicoccoides*) which is very important for the construction of the genealogy of wheats and which was not taken into consideration by Dr Zade, we cannot agree completely with the concluding genealogical table of wheats, given on p. 144. We believe that the difference in varieties which occurs in species of cereals cannot be neglected in genetic work.

The striking parallelism of fungal and "serum" reactions once more confirms the possibility of using both these methods for genetic and systematic purposes.

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