10 February 1961, Volume 133, Number 3450 **SCIENCE**

CURRENT PROBLEMS IN RESEARCH

Man-Guided Evolution in Plant Rusts

Through his modification of the host plants of the cereal rusts, man is also modifying the rusts.

T. Johnson

It is a commonplace that man's interference with nature results in modification of plants and animals. This is so well known that the subject scarcely merits discussion unless facts emerge that throw some light on the mechanism of the process of modification. The rusts of wheat and other cereals (and particularly stem rust, *Puccinia graminis*) are among the most important enemies of man's food crops. Within the last 40 years plant breeders have modified the wheat plant in such a way that, in certain of the more important wheat-growing areas, the modifications have greatly influenced the pathogenic properties of the rust parasites. The pathogenic response of the rusts to these changes are such that they can be causally related to the man-made modification of their hosts. This relationship would seem to be of sufficient biological interest to be worth reporting beyond the relatively small circle of specialists who have been directly concerned with these phenomena (*1*).

Cereal Rusts Prior to the Breeding of Resistant Varieties

As stem rust is economically the most important of the cereal rusts, and the one on which investigation has been concentrated, I will use it as the principal basis of discussion. It may be assumed that processes of variation applicable to this rust are also applicable to most other rusts.

The host species most frequently subjected to modification by breeding and selection is the 42-chromosome wheat, *Triticum aestivum* (= *Triticum vulgare*), which comprises the world's principal bread-making varieties. Before breeding for rust resistance was begun, the varieties of bread wheat grown by farmers in the various wheat-growing countries were susceptible to stem rust (Fig. 1). The earliest studies on the pathogenicity of stem rust, carried out in Sweden in the last decade of the 19th century by Jakob Eriksson (*2*), showed that the rust was not a single unit, pathogenically. Rust collected on wheat was pathogenic to wheat, barley, and certain grasses but attacked rye only slightly and oats scarcely at all. Rust collected on rye was pathogenic to rye, barley, and certain species of grass but not to wheat or oats. Rust collected on oats attacked oats and certain grasses related to that crop but was nonpathogenic to the other cereals. In general, it was clear that the rust was parasitically adapted to the host plant on which it was found. As the morphological differences between the rust samples collected on these plant hosts were so small as to be insignificant, Eriksson regarded these pathogenic variants as *formae speciales* of the rust species *Puccinia graminis*.

Stakman and his co-workers (*3*) showed that this pathogenic specialization was more narrowly restricted than had been suspected by Eriksson. They found that rust collected on given varieties of wheat was parasitically adapted to those varieties but not necessarily to other varieties. In consequence it was possible, by judicious selection of wheat varieties, to develop a series of "differential hosts" whereby numerous pathogenically distinct "physiologic races" of wheat-stem rust could be identified by means of the infection types produced on wheat plants in the seedling stage. Stakman and his collaborators showed, furthermore, that these physiologic races would remain constant in their pathogenic behavior over a period of many years and could therefore be regarded as relatively stable biological entities (*4*).

Breeding of Rust-Resistant Bread-Wheat Varieties

The discovery of physiologic specialization in wheat-stem rust had far-reaching practical implications. It was demonstrated that a given variety of wheat (such as Marquis) might be resistant to a large group of physiologic races but susceptible to another group. Another variety (such as Kanred) might be resistant to many of the races that could attack the first variety, though susceptible to other races. Both varieties would be susceptible in the field because of the multiplicity of rust races occurring in nature. The range of resistance could, however, be broadened by crossing the two varieties. Some of the plants descended from a cross would have resistance to more races than either parent. These plants could, in turn, be crossed with other varieties so as to broaden the range of resistance still further. Theoretically, it should have been possible, by a long

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series of such crosses, to produce a variety resistant to all or most of the races. But, as new races were found every year, it was found to be impracticable to produce totally rust-resistant varieties by this method.

In effect, the problem of producing rust-resistant varieties of bread wheat was solved by other means. In some of the major rust epidemics in the United States and Canada, from 1904 onward, it was observed that certain varieties of wheat were free from rust. These, however, were not bread wheats. They were either durum wheats (*Triticum durum*) or emmer wheats (*T. dicoccum*). The fact that both these species had 28 chromosomes instead of the 42 chromosomes of bread wheat cast doubt on the possibility of crossing these wheats with the bread wheats. Efforts were made by many plant breeders in North America, and these efforts eventually bore fruit in the production of a hybrid between the durum variety Iumillo and the bread wheat Marquis (*5*) and the production of a hybrid between the emmer variety Yaroslav and Marquis (*6*). In each case the hybrids had the appearance of bread wheats but had much of the rust resistance of the durum or emmer parent. These hybrids were later used in crosses with high-quality bread wheats, with the result that many rust-resistant spring wheats of good quality for breadmaking were distributed to farmers between 1935 and 1940 in the "rust area" of the Dakotas, Minnesota, and the Canadian Prairie Provinces. In the region subject to greatest rust damage these varieties totally replaced the older, susceptible varieties.

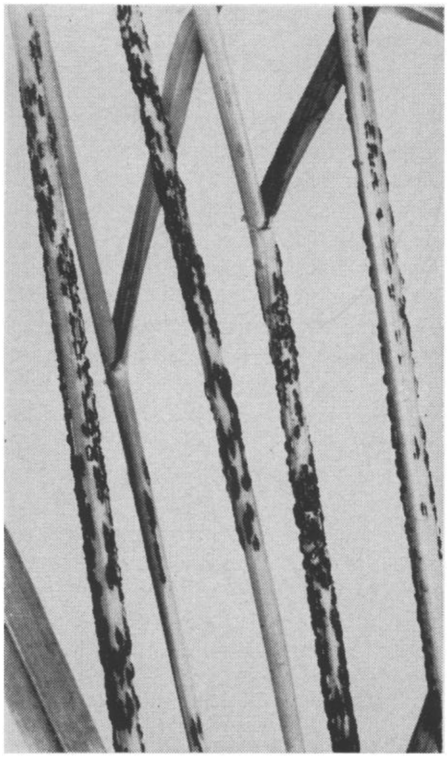


Fig. 1. A susceptible variety of wheat infected by stem rust in the uredial or summer stage.

General Characteristics of Rust-Resistant Varieties

In the first decade of this century Sir Rowland Biffen (*7*) showed that resistance of wheat to yellow rust (*Puccinia glumarum*) was inherited in accordance with Mendelian laws. Resistance was recessive to susceptibility and was inherited as a simple Mendelian recessive. This was a discovery of significance for rust research because it showed that resistance to rust could be separated from other plant characteristics and recombined with other desirable qualities. Biffen's classical work inaugurated the era of scientific plant breeding for resistance to the rusts.

H. K. Hayes and his students demonstrated that, in crosses between varieties of bread wheat, a single rust-resistance gene (as, for instance, the Kanred gene) might condition resistance to a large group of rust races. The introduction into bread-wheat varieties of resistance from durum and emmer wheats, however, showed greater practical promise because durum and emmer resistance genes conferred a much broader range of resistance. The demonstration (*8*) that stem-rust resistance derived from emmer wheat and governed by one or two genes gave protection against all the known North American races appeared for a while to nullify the practical importance of physiologic specialization. This type of broadly based resistance was effective only in the adult stage and hence was known as "mature-plant" resistance. Plants which were susceptible to some races in the seedling stage were resistant to all known races in the adult stage, and the mature-plant resistance was inherited quite independently of any seedling resistance these plants might possess. When varieties with mature-plant resistance were distributed to farmers in the late 1930's, many plant breeders were hopeful that the physiologic races of stem rust had been effectually checkmated.

Genetical Characteristics of the Rust

Craigie's discovery (*9*) of the function of the pycnia of the rusts elucidated the sexual mechanism of the rusts and made possible the hybridization of physiologic races (*10*) (Figs. 2, 3). It was demonstrated that new races were readily produced by hybridization, and that races found in nature were generally heterozygous for various characteristics. Further studies showed that some, at least, of the pathogenic characteristics were inherited in accordance with Mendelian rules of inheritance (*11*).

Flor's classical studies (*12*) with flax rust (*Melampsora lini*) made it clear that there was a relationship between the genes for pathogenicity in a rust and the genes for resistance in the host plant. If a host plant had a given gene for resistance, it could be rusted only by a race that had a corresponding gene for pathogenicity; but if a host had two genes for resistance, it could only be rusted by a race (or races) with the two corresponding genes for pathogenicity. This gene-for-gene relationship is plausible in view of the fact that races can only be identified by the rust-reactions of the host, which have been shown to be gene-conditioned whenever they have been studied genetically, and the further fact that resistance genes can be demonstrated in the host only by the use of appropriate rust races. Thus, the host-parasite interaction has a genetic basis in both the host and the rust.

In most races of flax rust, virulence (ability to rust heavily) is a recessive character. Therefore, a race heterozygous for pathogenicity to a given host is avirulent on that host. In heterozygous rust clones a mutation of the dominant gene to the recessive confers virulence on the race (*13*).

Thus far, Flor's studies have given the principal clue to the interrelation of host and parasite. Host varieties differ greatly in their physiological processes, which are conditioned by genes. Some of these gene-conditioned processes are incompatible with the growth of a particular rust on the host. Rust races also differ in their physiological processes, which likewise are gene-conditioned. Compatibility of the gene-conditioned physiology of the host with the gene-conditioned physiology of the rust leads to susceptibility—hence the physiological interlocking of the genes of host and parasite.

Response of the Rust to the Growing of Resistant Varieties

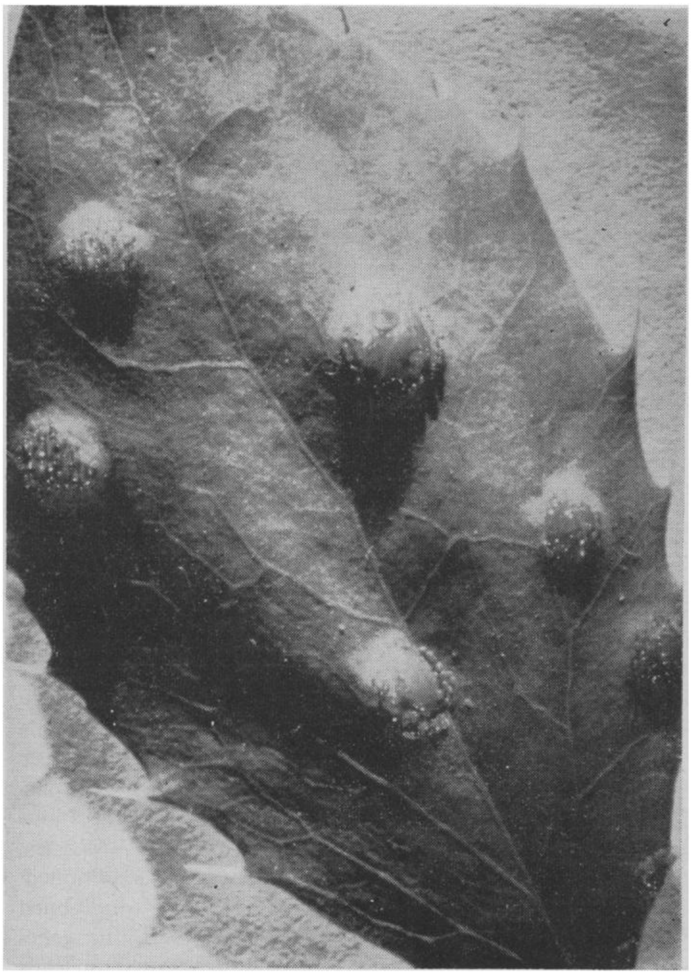
As was natural, the lead in producing rust-resistant varieties of wheat was taken in those wheat-growing areas in which stem rust was a particular threat. The areas in which varieties resistant to stem rust were first distributed were (i) the spring-wheat region of the United States and Canada, (ii) Australia, and (iii) Kenya Colony in East Africa. In these areas there was a sudden displacement of susceptible by resistant varieties of wheat. In the rust area of North America the acreage involved amounted to about 20 million acres.

The response on the part of the rust was somewhat similar in all these areas. After an initial period of freedom from rust, a few infections of a susceptible type began to appear here and there. These increased in number year by year until some varieties of wheat that had been resistant had to be regarded as susceptible. The rate of increase of rust development differed considerably in the different regions. In Australia, the variety Eureka, distributed in 1938, began to rust in 1941 and rusted considerably in 1942, after which date it was gradually replaced by other varieties. In North America, freedom from stem rust lasted from the period of distribution of the resistant varieties (1935–38) until 1950, when race 15B, first found in 1939, became relatively abundant in the Mississippi Valley. Thereafter, the increase of this race was rapid, culminating in the great stem-rust epidemic of 1954. In Kenya, a sequence of resistant varieties brought to light a sequence of rust races capable of attacking them.

The timing of the appearance of virulent races differed considerably in the different regions, as did also the pathogenic characteristics of the virulent races. These new races did not necessarily have a greater over-all virulence than the older races; their virulence was specially adjusted to the new resistant varieties.

Mechanism of Interaction of Rust and Host

Changes of pathogenicity in the rust appear to proceed stepwise with reference to the host genes for resistance. A new type of stem rust capable of attacking a formerly resistant variety is most commonly a variant of some common race, the variant being identifiable only by its ability to attack (render ineffective) the gene that made the variety resistant to the original race. To remain resistant for long a variety needs to have more than one resistance gene operating against the races prevalent in the region of its cultivation. Figure 4, adapted from one employed by Australian investigators (*14*), illustrates the stepwise process by means of which a



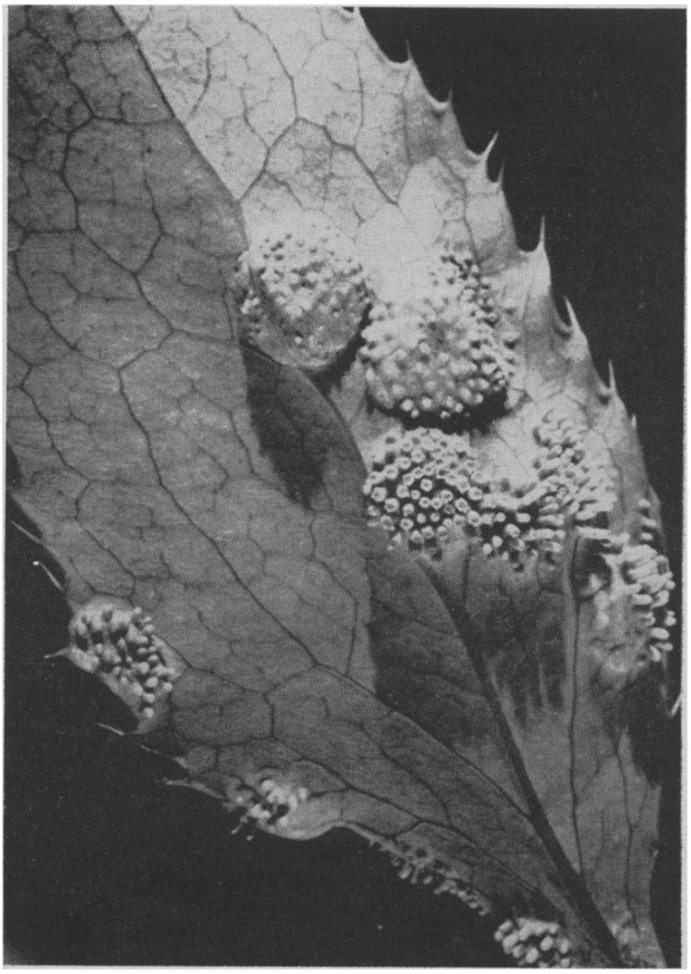


Fig. 2 (left). The sweet exudate of stem rust in the pycnial stage attracts insects, which are important agents in natural hybridization of rust races. Fig. 3 (right). Stem rust in the aecial or cluster-cup stage is a factory for the production of new races, of which only the best-adapted gain wide distribution.

race may overcome the resistance of a variety.

Two loci determining pathogenicity are assumed to be present in the rust race, and two loci determining resistance are assumed to be present in a wheat variety. The rust genes are not initially capable of affecting the resistance genes in the wheat. A mutation of rust gene *a* to *a'* will overcome the resistance effect of gene A in the variety, but the variety remains resistant because of the protective effect of gene B. For a similar reason mutation of *b* to *b'* does not affect the reaction of the variety. Mutation at both loci in the rust will affect both loci in the wheat and render the variety susceptible.

The type of thinking outlined above has considerably influenced the planning of wheat breeding programs. There are several possible procedures, all of which, of course, depend on the identification and isolation of genes for rust resistance. When a number of rust-resistance genes have been identified and segregated, they can be used in several different ways. They can be combined in pairs, as was done by the Australian breeders (*14*) (genes AB in one variety, CD in another, and so on), on the assumption that it is unlikely that rust races would simultaneously overcome several different types of resistance. Another procedure is the development of a multilineal variety in which various lines of the same morphological type contain different genes for resistance (*15*). In such a variety those lines that succumb to rust could be withdrawn and replaced by new lines as these become available. A third approach is the "pyramiding" of all available genes in the same variety in order to confer on that variety a maximum range of resistance.

Each of these processes is likely to produce its specific effect on the rust organism, and none is entirely free from objectionable features. The introduction of pairs of resistance genes is likely to give rise eventually to races with pathogenicity genes nullifying the resistance effect of the paired genes. The multilineal variety is likely to bring into being simultaneously a considerable variety of rust races and thereby increase the diversity of the gene pool of the rust. The variety containing all available resistance genes would become susceptible only to a race with a very wide range of pathogenicity, but the danger of encouraging the production of such a "super" race is obvious.

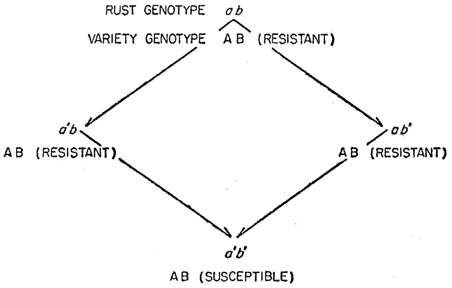


Fig. 4. Given two factors for resistance in the host, two corresponding mutations in the rust are necessary before the host becomes susceptible (see text).

No matter which plant-breeding procedure is adopted, it is clear that it will have a guiding influence on the pathogenic types of rust that eventually will appear in areas of large-scale cultivation of rust-resistant cereals. By his manipulation of rust-resistance genes the plant breeder is therefore guiding the evolution of pathogenic types in the rusts. Consequently, it is necessary to understand, as far as possible, the mechanism of the origin of new pathogenic types in the rusts and to correlate plant-breeding practices with that understanding.

Mechanism of the Origin of New Pathogenic Rust Types

Some acquaintance with the life cycle of stem rust is necessary to gain any understanding of how new pathogenic types originate. Stem rust is a heteroecious rust, spending part of its life cycle on cereals and grasses and part on certain species of barberry, of which the most important is common barberry, *Berberis vulgaris*. The repeating, uredial stage on cereals and grasses is followed, in autumn, by the telial stage. The spores of the telial stage survive the winter, germinate, and produce on the barberry the pycnial and aecial stages, which represent the sexual phase of the life cycle. The aeciospores re-initiate the repeating uredial stage on cereals and grasses.

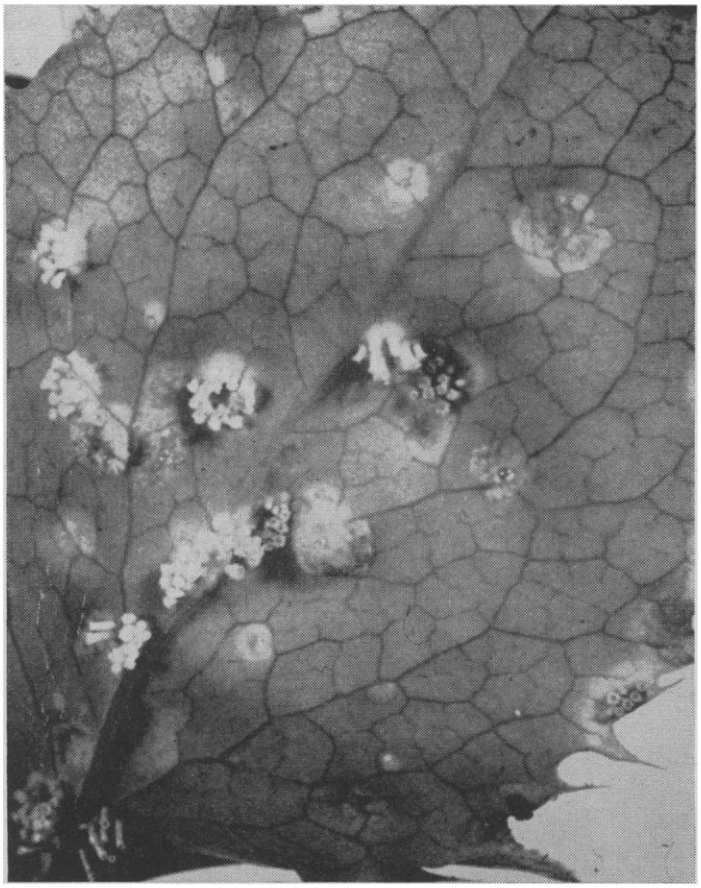
Cytologically, the uredial stage is dikaryotic, each spore containing two haploid nuclei. Fusion to form a diploid nucleus occurs in the telial stage, in the maturing teliospore. In the germination of the teliospore two divisions occur, one reductional and one purely mitotic, resulting in the production of four basidiospores, two of (+) and two of (−) mating type. As each basidiospore can give rise to a pycnium, the mating types of the pycniospores correspond with those of the basidiospores. For the production of aeciospores it is necessary to apply pycniospores of a (+) pycnium to a (−) pycnium, or vice versa. An aeciospore, therefore, contains a (+) and a (−) nucleus, and this dikaryotic condition is perpetuated in the uredial stage.

"Crosses" between races can be made readily by applying pycniospores of a (+) pycnium of one race to a (−) pycnium of another, or vice versa. The "selfing" of such a "dikaryotic hybrid" will produce many races displaying various combinations of the pathogenic characteristics of the races entering into the cross. The understanding of the sexual mechanism of the rust and its importance in the production of physiologic races was an important spur to the destruction of barberries in North America, of which some 500 million plants have already been eradicated.

It would be expected that the reduction in number of barberries in the Mississippi Valley area resulting from the active barberry eradication campaign carried out from 1918 onward would greatly minimize the creation of new races of rust by means of the sexual process. Nevertheless, new races were encountered frequently, and investigators began to suspect that other processes of variation must be at work in the creation of new pathogenic types of rust. Two such processes are known: mutation and heterokaryosis.

Many mutations, both spontaneous and artificially produced, have been recorded in the rusts (Fig. 5), and it is generally agreed that this fundamental source of variation is of great significance. Virulence is often a recessive character, and mutant genes undoubtedly accumulate in the uredial stage of the rust, to find expression after they have passed through the sexual phase on the barberry.

In recent years there has been considerable research effort to determine the possible significance of heterokaryosis in the origination of pathogenic types. Heterokaryosis per se, involving only the reassociation of haploid nuclei in uredial clones in contact with one another, is a less effective means of variation than hybridization. Two rust clones with nuclei A^+B^- and C^+D^-, respectively, can be expected to produce only the two recombinants A^+D^- and B^-C^+. Several studies on heterokaryosis (*16, 17*) have indicated a situation con-



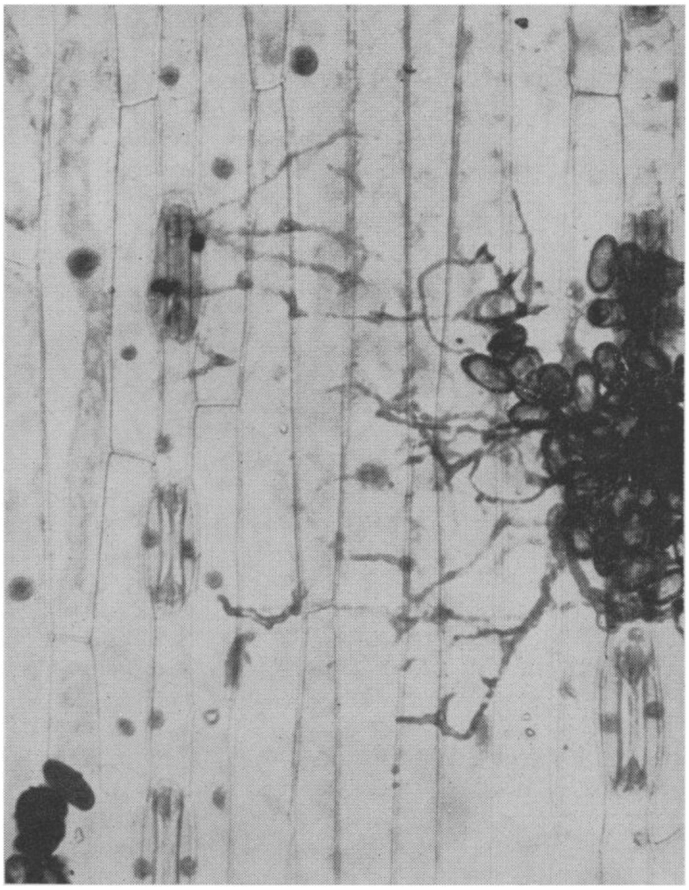


Fig. 5 (left). Mutation is a factor of importance in variation. In this photograph the white (mutant) aecia stand out in sharp contrast to the less conspicuous normal, yellow aecia. Fig. 6 (right). Germ tubes of uredospores often come into contact on leaf surfaces, or the mycelia which they produce after penetration may come into contact, thereby permitting nuclear exchange between different clones of the rust.

siderably more complex than that (Fig. 6). The large number of new pathogenic rearrangements secured from a combination of two clones suggests that some parasexual process must be at work. For this process Watson and Luig (*17*) have used the term *somatic hybridization*. Whether or not this process conforms to the parasexual processes outlined by Pontecorvo (*18*) is not yet known.

Although all the processes mentioned doubtless contribute to the production of new pathogenic types of rust, there is no good reason for assuming that hitherto unknown pathogenic types have come into being just before they were found. Nature must contain a large reservoir of pathogenic types that have not been detected by the physiologic-race surveys and other means of detection employed by the rust investigator. In addition, even the physiologic races already known must contain a pool of unexpressed genes for pathogenicity that may at any time come to light through sexual, heterokaryotic, or parasexual processes. The rust investigator and the plant breeder must therefore expect a continuing supply of previously unknown pathogenic types of rust.

The realization that there is a relationship between the genic constitution of the resistant host plant and the genic constitution of the rust race that may eventually attack it is of more significance for the plant-breeding methods of the future than for those of the past. For the last two or three decades plant breeders have been able to identify rust-resistance genes and separate them one from another. Initially the genes were identified and numbered without knowledge of the specific chromosomes on which they were located. More recently, through the brilliant work of Sears (*19*) and his collaborators, methods have been developed to determine on which chromosomes the genes are located. This knowledge, which is acquired by the use of nullisomic and monosomic lines, and the increasing use of backcrossing methods, make cereal breeding today much more precise than it has been in the past. These methods will probably permit the synthesizing of a host variety with almost any desired genic combination. But in so synthesizing a variety, due regard will have to be paid to the corresponding genic synthesis that nature is likely to bring about in the rust organism. The plant breeder cannot afford to forget that he is guiding the pathogenic evolution of the rust.

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Personality and Scholarship

The traits of able students at colleges productive of scholars are different from those of other able students.

Paul Heist, T. R. McConnell, Frank Matsler, Phoebe Williams

Objective studies of the product of the educational process in America's colleges and universities are relatively few. The report by Learned and Wood of a study of the "academic growth of the baccalaureate mind" is still the most comprehensive assessment of the output of higher education that has been published (*1*). Two decades ago they demonstrated amazing differences in achievement among the students attending the various colleges in a single state.

More recent landmarks are the studies by Knapp *et al.*, which showed that a relatively small number of higher institutions in the United States were much more productive of scientists and scholars than the great majority of colleges and universities. The index of institutional productivity devised by Knapp and Greenbaum was the number of students per thousand graduates from 1946 to 1951 who later received either (i) Ph.D. degrees, (ii) university fellowships, (iii) government fellowships, or (iv) private foundation fellowships exceeding $400 per year. Fifty institutions with the highest indices for male graduates and 13 with the highest indices for female graduates were designated as institutions of high productivity.

Knapp and Greenbaum suggested some reasons for the striking differences in educational productivity they discovered. Although they did not disregard the quality of the students attracted to the most productive colleges in attempting to explain the institution's records, they nevertheless put the greater emphasis on the institutions—the faculty, the objectives, and the intellectual atmosphere. In referring specifically to the exceptional productivity of a few small liberal arts colleges, they spoke of their "singular hospitality to intellectual values in general" and declared that "the climate of values sustained by the institutions elevated the scholar and intellectual to the position of 'culture hero' " (*2*).

While serving as a member of a planning committee for research on diversification of American higher education at the Center for the Study of Higher Education of the University of California, Berkeley, Darley shifted the explanation for differential productivity from the institution to the student when he said (*3*): "Without cynicism, one might state that the merit of certain institutions lies less in what they do to students than it does in the students to whom they do it."

Subsequently, a study by Holland (*4*) lent support to this hypothesis. After comparing certain characteristics of National Merit Scholarship winners and near-winners who attended colleges having "high" and "low" indices of productivity, he concluded that differential institutional productivity is a function of the concentration in certain institutions of exceptionally able students with high scholastic motivation. Holland, in another study, also found that the parents of National Merit Scholarship students who attended colleges which ranked high in productivity placed a high value on "learning how to enjoy life, and developing mind and intellectual abilities," while those whose children went to colleges which ranked lower placed less emphasis on intellectual goals (*5*).

In several research projects the Center for the Study of Higher Education has explored the hypothesis that particular colleges and groups or types of institutions are differentially selective, not only with respect to scholastic aptitude but also with respect to attitudes, values, and intellectual dispositions. The study reported here was devised to test the general hypothesis that highly productive institutions, by the criteria of Knapp and Greenbaum, are more attractive than less productive ones to National Merit Scholarship students with high scores on certain personality tests designed to measure attributes closely related to intellectual orientation and intellectual functioning.

The Sample

The population of students of high ability from which the sample for the study was drawn consisted of all the winners and a 10-percent sample of those who received certificates of merit (the near-winners) from the National Merit Scholarship Corporation in the

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