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STABILIZING SELECTION IN *Puccinia graminis tritici*

by

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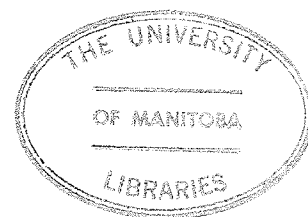
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A B S T R A C T

The competitive abilities of seven related races of *Puccinia graminis* f. sp. *tritici* were studied on three to five susceptible wheat varieties by serial inoculations in greenhouse and growth cabinets, and by natural spread from artificial infection foci in field plots. In relation to the concept of stabilizing selection, the susceptible wheat varieties met the criteria for a simple host, and races with few virulence genes and those with many met the criteria for simple and complex races, respectively. In each of three models studied three different race mixtures were made. In two models one race was a simple race and the other a complex race. The races studied in the third model had equal numbers of virulence genes. In those models with simple and complex races, complex races predominated after 4 to 10 generations in five mixtures, whereas, the simple race predominated in one mixture. In the field experiment a complex race predominated over the simple race.

It was concluded that virulence genes did not impair the competitive abilities of the races of the wheat stem rust fungus studied and that simple genetic control of virulence alone does not contribute to superior competitive ability.

Temperature did not differentially influence the competitive abilities of the races in three mixtures studied in the growth cabinets. In a fourth mixture the complex race predominated at 25°C and the simple race at 15°C.

Pustule age did not affect urediospore germination significantly.

Urediospore germination was slightly higher for races C18(15B-1L) and C33(15B-1L) than for races C9(15B-1L), C37(15), C38(15B-1L), C42(15) and C49(15). Temperature affected the length of the incubation period but races C18(15B-1L) and C33(15B-1L) developed faster than races C9(15B-1L), C37(15), C38(15B-1L), C42(15) and C49(15) at all temperatures. In addition, races C18(15B-1L) and C33(15B-1L) had a shorter incubation period than the other races and produced significantly more spores per pustule than races C9(15B-1L), C37(15) and C49(15). The differences in incubation period and spore production are considered to be most important and they could account for the differences in aggressiveness of the seven races studied.

The hypothesis that races with wide host range lack fitness to survive in the field was proposed by Flor (1953, 1956) for *Melampsora lini* (Ehrenb.) Lev. Races with few virulence genes on the other hand were isolated frequently from field collections and were more fit to survive. Similarly, Watson (1958), in Australia, concluded that races of *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. with wide host ranges were unable to maintain themselves in mixtures with races of narrow host range when grown on susceptible seedlings in the greenhouse. He observed that races with narrow host ranges were isolated more frequently from field collections than races with wide host ranges. Van der Plank (1968) proposed a concept of stabilizing selection to explain how reduced fitness to survive is presumed to result from unnecessary genes for virulence and this prevents virulent races from becoming predominant on simple varieties.

In van der Plank's (1968) terminology, a wide-host-range race is analogous to a complex race, and a narrow-host-range race is analogous to a simple race. He described stabilizing selection as the predominance of simple races over complex races on simple varieties. A simple race of a pathogen was described as one that can only attack varieties without genes for vertical resistance and, therefore, has few, if any, genes for virulence. A complex race has many virulence genes that enable it to attack complex varieties with many resistance genes.

According to van der Plank (1966) when plant pathogens are isolated from a field of susceptible hosts the majority of isolates should be races with few genes for virulence. Most races from a field of

resistant hosts should be relatively simple races with the minimum number of virulence genes necessary to attack those hosts. This means that the fittest races of a pathogen are those with just enough virulence to attack the predominant host variety.

Van der Plank (1968) distinguished between weak and strong resistance genes. Stabilizing selection occurs for virulence on strong genes but not on weak genes. He speculated that races of *P. graminis* f. sp. *tritici* able to attack wheat varieties with strong genes, for example *Sr6* and *Sr11*, lose fitness to survive on hosts without those genes. Races virulent on a weak resistance gene are often common and are fit to survive on hosts without that gene. Vertical resistance genes *Sr8* and *Sr15* are weak genes because all Australian races were virulent on them although no Australian variety carried them. Van der Plank believed that stabilizing selection was an important consideration in the deployment of strong resistance genes. He suggested the use of simple varieties in the southern United States and the planting of varieties with strong vertical resistance genes in northern United States and Canada. Planting simple varieties in the south would favour simple races. Complex varieties planted in the northern areas would not be damaged by simple races moving northward.

Van der Plank's proposals have stimulated research with conflicting results on the validity of his concept of stabilizing selection. The proposals, if true, have scientific and practical significance, but the contradictory results necessitate further investigations. The study described here was designed to determine whether unnecessary virulence genes are harmful to Canadian races of wheat stem rust and to investigate

the effect of environmental conditions such as temperature on the survival ability of races with different numbers of virulence genes.

2.

LITERATURE REVIEW

2.1 SURVIVAL ABILITY AND STABILIZING SELECTION

Survival ability and stabilizing selection are not considered synonymous. Survival ability of a race will be used to designate the ability to survive and cause disease in competition with another race. Survival ability is used here because it is an important factor in stabilizing selection.

2.1.1 *Phytophthora infestans*

Black (1952) studied race mixtures in *Phytophthora infestans* (Mont.) de Bary and found that the wider the host range of a race, the lower its survival ability in competition with a race with a narrower host range on susceptible potato varieties. These results were similar to those obtained by Thurston and Eide (1952, 1953) who cultured races of 0 and 1 for 4 and 8 generations on susceptible potato varieties in the greenhouse. After 4 generations race 0 was the predominant race and after 8 generations the proportion of race 0 to race 1 was 90:1.

Thurston (1961), working with *P. infestans* in the greenhouse, mixed about equal proportions of race 0 and race 1, race 0 and race 4, race 0 and race 1,4, race 0 and race 2,4, and race 0 and race 1,2,4, and grew the mixtures on susceptible potato clones. After up to 9 generations race 0 predominated over the other races with wider host ranges. These results agreed with the observed high frequency of race 0 in the field.

Thurston (1961) also studied the ability of 5 races of *P. infestans* to spread in the field. He inoculated different plots of a susceptible variety separately with each one of the five races. Relative fitness

was determined by comparing rate of spread of the races in the plots. Race 2,4 with two unnecessary virulence genes, spread most rapidly. It was followed by race 1, with one unnecessary virulence gene, and then by race 0 without unnecessary virulence genes. He suggested that the difference between the greenhouse and field results was caused by different isolates of a race having different aggressiveness and he implied that virulence and aggressiveness are independent. He did not speculate on the effect of different environments on aggressiveness.

2.1.2 *Trichometasphaeria turcica*

Scheifele, Nelson and Wernham (1968) determined the survival ability of races of *Trichometasphaeria turcica* Lutt. in mixtures propagated for several generations on simple inbred lines of corn with no genes for vertical resistance. They used monoconidial isolates 13a and R58 of *T. turcica* from corn. These isolates were equally virulent on the susceptible inbred number 4. Isolate 13a had the fewest genes for virulence; R58 had more genes for virulence than 13a. In a second experiment they mixed isolates R58 and T8 on inbred number 4. Isolate T8 had more genes for virulence than isolate R58. In the first mixture, the simple isolate predominated within three generations, whereas, the complex isolate predominated in the second mixture after four generations. They suggested that other biological attributes of the organism, entirely independent of the genes for virulence, govern the success or failure of a race to survive in a given mixture during the parasitic phase of the fungus.

The idea that factors governing fitness to survive in the parasitic phase of nonobligate parasites are independent of genetic simplicity or

complexity of the pathogen was supported by the studies of Scheifele and Nelson (1970). Using similar methods and materials (isolate R60 used instead of T8) to those used in the previous experiment, they determined the differential survival abilities of three isolates of *T. turcica*. They obtained results similar to those of the previous experiment. Increased infection and sporulating efficiency and a decreased incubation period were fitness attributes associated with the predominant isolates in each mixture. They concluded that genetic simplicity for virulence could not account for the survival fitness of the simple race.

2.1.3 *Fusarium oxysporum*

Van der Plank (1968) used the example of races 1 and 2 of the tomato wilt fungus to explain stabilizing selection in nonobligate parasites. Resistance gene I confers resistance to race 1 but not to race 2. He stated that Fusarium wilt, incited by *Fusarium oxysporum* Schlect. f. sp. *lycopersici* (Sacc.) Snyder and Hans. race 2, is unlikely to menace the tomato (*Lycopersicon esculentum* Mill.) crop as race 1 did prior to the introduction of varieties with gene I. He concluded that race 2 had occurred often and could have become common, but stabilizing selection prevented its increase. Race 2 was held in check by the tomato varieties possessing the resistance gene I. Gene I is a strong gene that enabled stabilizing selection to reduce the incidence of race 2.

Crill *et al.* (1973) demonstrated that Fusarium wilt, incited by race 2, is a very serious disease of tomato in the second year land production areas of Florida. The occurrence of race 2 of Fusarium wilt in

land which had been cropped only two seasons to the susceptible variety Homestead 24 varied from 43% to 74%. They concluded that race 2 of *Fusarium wilt* is as serious a menace to tomato production as race 1 had ever been. They indicated that stabilizing selection, as reported by van der Plank, did not exist with respect to *Fusarium wilt* of tomato caused by race 2.

2.1.4 *Puccinia striiformis*

Brown and Sharp (1970) produced evidence to show that a complex race of this rust can predominate over a simple race on the susceptible wheat varieties Lemhi and Hana. The complex race with many unnecessary genes for virulence had greater survival ability than the simple race without unnecessary genes for virulence. Their results questioned the proposal that there is always a negative correlation between survival ability and the number of genes for virulence present.

2.1.5 *Puccinia recondita*

Irish (1950) studied competition among physiologic races of leaf rust of wheat, *P. recondita* Rob. ex Desm. f. sp. *tritici*. He found that races 9 and 15 dominated in a mixture of races 9, 15, 58 and 126 on the variety Cheyenne. Race 15 has the narrowest host range followed by race 9 on the old differential hosts (Johnston, 1961).

Aslam and Browder (1971) studied the relationship of aggressiveness to pathogenicity in *P. recondita* f. sp. *tritici* in three cultures; 66 - 763, virulent at 8 out of 12 loci studied; UN01 - 68A, virulent only at the *P_{Lr10}* locus; and UN01 - 68B, virulent at all loci studied. Survival in mixtures, relative infectivity, and urediospore production were used as criteria for aggressiveness. Three composites of two

cultures each were grown for several generations on Bison wheat, which has no known genes for resistance. A high positive correlation was found between the cultures with few genes for virulence and survival in mixtures. The cultures also differed in infectivity on Bison with the most avirulent culture being significantly more infective. However, Watson (1970) has shown that unnecessary genes for virulence are not lost from a fungus population. He reported that the most prevalent races of *P. recondita* f. sp. *tritici* in Australia are 68-1,2,3,4 and 76-2,3. Race 76-2,3 has few unnecessary genes for virulence and is able to attack the commonly cultivated wheats. Strain 68-1,2,3,4 has virulence which is not necessary for survival. He concluded that if a gene for virulence has no deleterious effect and is associated with genes for aggressiveness and survival ability in a well-adapted race, it may remain in the population whether it is necessary or not.

2.1.6 *Puccinia graminis avenae*

Leonard's results (1969) strongly support the van der Plank concept. He used a heterogenous population of *P. graminis* Pers. f. sp. *avenae* Eriks. and E. Henn. from collections of overwintered telia on orchard grass (*Dactylis glomerata* L.). Small barberry plants were inoculated in the greenhouse by suspending infected orchard grass stems over plants in a moist chamber. Susceptible Craig oat plants were inoculated with an aqueous suspension of aeciospores obtained by grinding the aecial tubes in water. He cultured the heterogenous population for eight uredial generations on the varieties Craig and Clintland A in the greenhouse. Races producing avirulent infection types on the oat stem rust differential hosts increased in the population. Races virulent on

particular varieties had survival values 14 - 46% lower than those avirulent on the same differential varieties. He concluded that the barrier to the built up of races with many genes for virulence is their inability to compete with races with few genes for virulence.

A question inherent in Leonard's work is whether a population from *D. glomerata* is representative of oat stem rust. A population from oats might have behaved differently from the one he used which may have had a long association with *D. glomerata* and barberry. Indeed, Roane *et al.* (1960) showed that those races of *P. graminis* f. sp. *tritici* isolated from aecia or from uredia in the vicinity of barberry bushes may have relatively low survival ability in comparison with other races.

Despite the relationship between survival ability and genes for virulence in *P. graminis* f. sp. *avenae*, indicated by Leonard's work, some recent reports indicate that the relationship is not real. Race 31 of oat stem rust is now the most common race in North America (Martens *et al.*, 1970; Stewart and Rothman, 1971). Since race 31 and other North American races carry several unnecessary genes for virulence Martens *et al.* (1970) concluded that unnecessary genes for virulence do not necessarily reduce competitive ability. Martens (1973) studied mixtures of races of oat stem rust in growth cabinets at 15^o, 20^o and 25^oC and in the field. The races with fewest genes for virulence maintained or increased their levels in the growth cabinets in all cases, but were consistently outperformed by races with many genes for virulence under field conditions. The data indicated that genes for virulence, other than those required for successful parasitism, are probably not important factors influencing the rise or decline of

any one race of oat stem rust in the field. He stated that an inverse relationship between the number of genes for virulence in the pathogen and its competitive ability, while it may occur in some cases, is not a general rule for host-parasite systems.

2.1.7 *Puccinia graminis tritici*

Watson (1942) selected races 17, 19, 34, 56 and 147 of wheat stem rust, *P. graminis* f. sp. *tritici*, and studied their development singly and in association with others. He cultured various mixtures of races on seedlings of susceptible varieties of wheat for five generations in the greenhouse. Watson found that race 34 with the widest host range on the standard differentials, predominated when associated with the other races, whereas, race 147 with a narrower host range was always virtually eliminated from such mixtures after five uredial generations. He suggested that the amount and character of each race in the mixture, the variety on which the mixture was cultured, and the effect of temperature on the fungus might be responsible for these changes. In field plots, where epidemics of stem rust were produced by inoculating border rows of susceptible varieties with a mixture of a large number of races, he found that less than half the races used in the initial inoculations were recovered from the plots during the season, indicating that certain races had better survival ability than others.

Loegering (1951), in a similar experiment to Watson's, obtained similar results in the greenhouse but different results in a field experiment. The field observations indicated that race 56, a race with the smallest number of virulence genes on the standard differentials (Stakman *et al.*, 1962), increased more rapidly than race 17 on Ceres wheat, and

race 19 increased more rapidly than race 17 on Mindum. Race 17 has the widest range of virulence genes on the standard differentials among the races he used. On the varieties Fulcaster and Little Club in the greenhouse, race 17 consistently increased more rapidly than races 19 and 56 when grown in mixtures for several generations. Obviously these races increased at different rates on different varieties when grown in mixtures, even though the varieties appeared to be equally susceptible. Loegering stated that the relative ability of races to increase in mixtures is due not only to observable differences in virulence but also to relatively minor ecological factors, which, when operating together, affect the success or failure of physiologic races in nature. Browder (1965) found that race 56 with a narrower host range was more aggressive than race 15B with a wider host range when grown on susceptible varieties. He stated that the relative prevalence of races 15B and 56 in the United States, particularly in the hard red winter wheat region, agreed with the hypothesized association of aggressiveness with the minimum number of virulence genes required for survival.

Keed, as cited by Watson and Luig (1968), studied the differential survival of races 21-7 and 21-1,2,3,7 of wheat stem rust in the greenhouse on host plants which were equally susceptible to both races. The two races differed in their virulence on host seedlings, having one of the following genes: *Sr6*, *Sr11*, *Sr9b*, or *Sr15*. Race 21-1,2,3,7 which is virulent on seedlings having all four of the mentioned genes in combination, was mixed in three initial amounts with race 21-7 which is virulent on seedlings with *Sr15* alone but avirulent on other combinations of these genes. The mixture was propagated for four uredial generations. Regardless of the initial mixture complex race 21-1,2,3,7

predominated after four generations. This evidence showed that, under the conditions of her studies, the race with fewer genes for virulence was the poorer competitor.

Ogle and Brown (1970) compared the survival ability of wheat stem rust races 21-2,7 and 21-2,3,7 on eight wheat varieties. Race 21-2,7 possessed virulence genes to match resistance genes *Sr11* and *Sr15* while race 21-2,3,7 carried an additional gene for virulence on *Sr9*. Four of the test varieties had no resistance genes, and two carried resistance gene *Sr15*. Race 21-2,3,7 with one extra gene for virulence predominated, and at the end of the third generation constituted 90 - 99% of the population on all test varieties. A survey in Canada (Green, 1971a) of the prevalence of races of *P. graminis* f. sp. *tritici* during a 50 year period, showed that virulent races with unnecessary virulence genes have predominated. Green concluded that there is no evidence that unnecessary virulence is harmful or that stabilizing selection is operative in Canada, nor is there evidence that virulence on resistance genes *Sr6* and *Sr11* is harmful to the rust, although according to van der Plank (1968), they are strong resistance genes.

Luig and Watson (1970) have shown that in the Western Australia area two strains of *P. graminis* f. sp. *tritici* were present in 1961 viz. 21-2 (virulent on *Sr11*) and an apparent mutant from it, 21-1,2 (virulent on *Sr6* and *Sr11*). The mutant was favoured in the severe stem rust outbreak of 1963 by the cultivation of wheats with *Sr6* and it emerged as the dominant strain in that region over the next years despite a reduction in the acreage sown to the variety Eureka with *Sr6*. The virulence of the mutant 21-1,2 on plants with *Sr6* and *Sr11* gave it little selective advantage, but Luig and Watson assumed that virulence genes were combined

with those for aggressiveness which made the mutant an effective competitor.

The experimental data reviewed above indicate that virulence genes are not deleterious to the wheat stem rust pathogen.

2.2 FACTORS INFLUENCING SURVIVAL ABILITY

In attempting to explain the racial changes observed in nature, factors other than virulence genes and varietal reactions are very important. Knowledge of how environmental conditions affect survival abilities of different races could be helpful in explaining why one race is a better competitor than another in nature.

2.2.1 TEMPERATURE

The influence of the environment, especially temperature, on the development of *P. graminis* f. sp. *tritici* has been reported by Katsuya and Green (1967). They observed that in experiments on the competitive abilities of races C10(15B-1) and C17(56), predominance of a race in mixed infections was greatly influenced by temperature. Race C17(56) usually predominated over race C10(15B-1) in mixtures at higher temperatures but not at low temperatures.

Cassel (1939) studied the effect of temperature (2°, 9°, 20° and 30°C) on the germination of urediospores and the development of germ tubes of races 11, 34, 36, 38 and 56 of *P. graminis* f. sp. *tritici*. The optimum temperature for most races was 20°C followed by 9°, 30° and 2°C. Spores of race 34 germinated better than those of other races over a wide temperature range, but its germ tube growth was poorest at 20°C. Cassel concluded that on the basis of spore germination race 36 was