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STRATEGIES TO BE USED IN THE STRUGGLE BETWEEN RESISTANCE AND VIRULENCE GENES

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Abstract

STRATEGIES TO BE USED IN THE STRUGGLE BETWEEN RESISTANCE AND VIRULENCE GENES.

The cultivation of wheat varieties resistant to diseases such as stem and leaf rusts. mildew and septoria plays an important role in modern agriculture. However, the problem of how to keep varieties resistant for a long period has not yet been solved. Whatever type of resistance (specific, non-specific, tolerance etc.) the breeder chooses to use in his breeding work, the resistance stability will depend very much on the strategy used. There are many different approaches: (i) To introduce single specific factors into the cultivated varieties; (ii) To introduce the maximum number of factors in the same variety; (iii) To create multiline varieties; (iv) To cultivate different varieties carrying different resistant factors. Such a "mosaic" artificially creates, as in the case of multiline varieties, conditions similar to those which we find in wild populations. The use of multiline varieties and of "mosaic" varieties stresses the need for finding a greater number of different genes for resistance. At present we know that a large number of genes for resistance to rusts and to mildew is available in bread and durum wheats and in related species.

At present, stem and leaf rusts, mildew and leaf blotch are the main wheat diseases we breeders are facing in Italy. Diseases like *Helminthosporium, Fusarium,* yellow rust and bunt are, on the contrary, for the moment only a minor problem since their presence is limited and since some of them can be effectively controlled by non-genetical means. However, the continuous changes which have taken place in our agriculture during recent years do not permit us to discard the possibility that some of these diseases, or others, will become a serious problem in the future. We have to keep in mind what has happened in the last 10 years with mildew, *Fusarium* and leaf blotch, following the cultivation of new wheat varieties and the modification of crop management practices. The better, and especially the increased use of fertilizers, have favoured the development of mildew, while absence of rotation has created favourable conditions for *Fusarium* and other soil-borne parasites. Absence of rotation and especially the cultivation of new semi-dwarf durum wheats derived from Norin 10 have likely been responsible for the increased incidence of leaf blotch.

There are several ways to control diseases, but, without doubt, against parasites such as rusts and mildew, genetic control is the most effective. Much remains to be solved in this field, however, since the problem of how to keep varieties resistant for a long period has not yet been solved. In this respect it is interesting to note that, in the course of time, a certain equilibrium has been reached between the heterogenous wild populations and those of its parasites, which does not allow diseases to spread epidemically (Browning [1]). This equilibrium is difficult to obtain when a genetically uniform variety is put before heterogenous parasite population: there is an evident conflict between the nature of modern varieties and the necessity to avoid or to diminish the evolutionary processes of the parasite.

In fact it is the uniformity of cultivated varieties themselves which favours the appearance of new virulence factors. Consequently, whatever type of resistance (specific, non-specific, tolerance etc.) the breeder chooses to use in his breeding work, he will be obliged to use it with a dynamism equal to or superior to that which is characteristic of the parasites on account of their natural evolution. The latter, as we know, is often in direct relation with the resistance genes introduced in the varieties (Vallega [2]).

Therefore, to control diseases effectively with the use of resistant varieties, it is of fundamental importance to study more deeply the causes which modify this resistance, especially the role played by the appearance of new virulent races, and to have continuously at our disposal new resistant sources of different genetic origin (Vavilov [3]). This will permit us not only to substitute rapidly the resistance obstacles already overcome by the parasite, but also to create among the cultivated varieties a heterogeneity similar to that existing in the wild populations.

Another aspect we have to consider is the type of resistance to be used: the choice of one type or another will depend essentially on the problems to be solved and the conditions in which the varieties will be cultivated. Therefore, it is indispensable to study more deeply the factors which determine the different types of resistance in the host and the ecological situation of the parasite in a given region.

In Italian conditions stem rust has a brief period of survival on the plants, so that many of these escape natural infection. This clearly makes it difficult to select effectively for adult-plant resistance (Robinson [2A]). On the contrary, this type of selection is possible with leaf rust which, on account of the propitious conditions existing for its development, causes prolonged natural infections.

On the other hand, it is important to note that the use of a certain type of resistance does not exclude that of another. On the contrary, the concomitant use of more than one type of resistance permits a more stable and durable protection, which can more easily prevent the evolution of the parasite. For this

TABLE I. REACTION TO RACES OF *Puccinia graminis tritici* OF SOME LINES DERIVED FROM Fr K58–NT II 50.35 AND THEIR PROBABLE GENOTYPES

VARIETIES or LINES	GENES INVOLVED					REACTION RACES 34	CULTURES 21	14
Frontana K58-NT II 50-35	Sr_5	Sr_6	Sr_8	Sr_9	(Sr_{11}?)	0	0	0
Derivative Lines	Sr_5	Sr_6	Sr_8	Sr_9	(Sr_{11}?)	0	0	0
	Sr_5	Sr_6	Sr_8	Sr_9	—	1	0;1	0;
	Sr_5	—	Sr_8	Sr_9	—	4	0;1	0;1
	—	—	Sr_8	Sr_9	—	4	4	0;1
Victor	Sr_5	Sr_6	Sr_8	Sr_9		1	0;	0;

reason it is also important to use the land varieties in our breeding programmes since through many years of cultivation these varieties have acquired resistance, and especially tolerance, to a number of diseases.

The solution of the problem of the resistance stability also depends very much on the strategy used in the breeding work.

The different approaches proposed in the past have been clearly summarized by Vallega [4]:

(1) To introduce in the cultivated varieties specific factors with a wide range of resistance, which should be substituted once they become ineffective.

There are cases in which resistance has been maintained for a long period and many others where it has been lost rapidly.

(2) To introduce the maximum number of factors in the same variety. This approach has been widely used, but we have to keep in mind that when the virulence factors necessary for giving evidence of the corresponding resistance genes are not available, it is rather easy to lose some of the latter. This "genetical erosion" is very frequent and we have had several cases in our own material.

The line Frontana, K.58-NT II 50–35, for instance (Table I) is a variety which has been shown to be resistant in many parts of the world, and seems to have no less than five resistance factors (Sr_5, Sr_6, Sr_8, Sr_9, Sr_{11}) effective with respect

TABLE II. REACTION TO RACES OF *Puccinia graminis tritici* OF SOME LINES DERIVED FROM YUMA, AND THEIR PROBABLE GENOTYPES

	GENES INVOLVED	REACTION TO RACE CULTURES 14	14IT1	21	34	116	212
YUMA	A B C D	R	R	R	R	R	R
SINGLE GENES PRESENT IN YUMA	A	R	R	R	R	R	R
	B	S	S	R	R	R	S
	C	R	R	R	R	S	S
	D	S	S	R	R	S	R
LINES DERIVED FROM YUMA	A B C D	R	R	R	R	R	R
	A	R	R	R	R	R	R
	B C D	R	R	R	R	R	R
	B D	S	S	R	R	R	R
	B C	R	R	R	R	R	S
	C D	R	R	R	R	S	R

to the races of *Puccinia graminis* present in Italy (Zitelli and Vallega [5]). Through back-crossing we have tried to transfer all these factors to some Italian bread wheat varieties; genetical analysis made on the offspring has shown that not all these had inherited all the factors carried by the parental variety. This was because we did not have the indispensable virulent factors at our disposal.

A similar erosion during the selection process has happened with the durum wheat Yuma (Tables II, III), which has been shown to have (Zitelli and Vallega [6]) at least four resistance factors with respect to *Puccinia graminis*. In fact, only some among the lines derived from crosses with susceptible varieties have inherited all these factors, whereas others are susceptible to some races.

(3) A third approach is to create multiline varieties (Borlaug [7]) composed of morphologically similar lines, but carrying different resistance factors, and eliminate those lines which become ineffective. The breeding of such varieties, however, takes much time and work and, because of its conservative nature, it is

TABLE III. GENETIC EROSION DURING THE BREEDING PROCESS

VARIETIES OR LINES	REACTION TO RACE CULTURES 14	14IT1	21	34	116	212
YUMA	R	R	R	R	R	R
GERARDO LINES	R	R	R	R	R	R
	S	S	R	R	R	R
	R	S	R	R	R	R
LD 390	R	R	R	R	R	R
GIORGIO 302	R	R	R	R	R	R
GIORGIO Lin.	R	R	R	R	S	R

not possible to go further than the variety itself. In many countries, including Italy, this kind of variety is difficult to register. On the other hand, multiline varieties have, besides other important advantages, also the advantage of inhibiting the spread of the parasite between susceptible components through the presence of resistant plants.

(4) The cultivation of different varieties carrying different factors of resistance, so that there will be a wide range of resistant factors (Vallega [8]) in the whole cultivation area. Such a "mosaic" artificially creates, as in the case of multiline varieties, conditions similar to those which we find in wild populations. We are orienting our breeding work along this line, which we think has some important advantages with respect to multiline varieties. Briefly, these can be summarized:

(a) Owing to the fewer eventual back-crosses needed, it can be accomplished in a relatively shorter time and with less cost;

(b) At the same time, it permits the varieties to be improved for other traits;

(c) The increased genetical heterogeneity diminishes the risks due to spread of other diseases;

(d) It does not encounter difficulties arising from legal aspects in countries like Italy.

(e) Single varieties which reveal themselves as no longer resistant can be substituted independently of others.

The use of different varieties carrying different resistance factors limits the spread of the parasite; thus, it protects the average national production, even if only partially that of individual farmers.

Breeders, although working independently and pursuing different goals, but introducing different resistance genes, would be greatly aided in their work if there were an institute capable of continuously supplying information on as many sources of resistance as possible.

This institute should possibly also incorporate new resistance factors in local genetical backgrounds already adapted to the environment and to the important or potentially important parasites.

The use of multiline varieties and of "mosaic" varieties stresses the need of finding a greater number of different genes for resistance. Not only is the identification of the factors present in a certain source and their inheritance mechanism significant, but also their chromosomal localization.

Information about such a localization may be of use, especially for non-specific resistance factors, since it allows the transfer of these factors by cytogenetic means, which in certain cases are more dependable than the traditional field selection methods. This approach has been adopted in the case of chromosome substitution ($5B^S$, $7B^S$) that carries plant resistance to yellow rust in the variety Bersèc (Law and Johnson [9]).

At present we know that a large number of genes for resistance to rusts and to mildew is available both in bread and durum wheat.

For *Puccinia graminis* (Table IV) 28 genes have been detected: of these 23 are localized in chromosomes. (McIntosh [10, 11].)

For Italy, remarkably important are the genes present in Khapli, (Sr_{13}, Sr_{14}), in Kenya Farmer (Sr_{11}) and in Kenya 58 (Sr_6).

Specially interesting is the Sr_8 gene detected in Mentana, (Watson and Luig [12]) a variety which already in 1940 exhibited resistance factors with the appearance of race 15B (Vallega [13, 14]). Such a gene present in the majority of Italian varieties of bread wheat is an interesting source of resistance for some biotypes of race 14 (Vallega and Zitelli [15], Zitelli [16]). Such biotypes, which are spreading rapidly in southern Italy and in the Mediterranean area, are turning out to be virulent on some new durum varieties. This applies, for example, to Valgerardo, a variety which although resistant to all rust races, has lost, during selection processes, the corresponding resistant factors derived from Yuma (Zitelli [17]).

TABLE IV. GENES FOR STEM RUST RESISTANCE *(from McIntosh,* [10, 11])

Genes.	Chromosome.	Varieties
Sr_{21}	2 A	EINKORN (T. Monococcum)
Sr_{23}	4 A	ETOILE DE CHOISY; SELKIRK
Sr_{8}	6 A	RED EGYPTIAN; MENTANA; FRONTANA
Sr_{13}	6 A	KHAPSTEIN; GIORGIO 302; KHAPLI (T. Dicoccum)
Sr_{26}	6 Aβ	EAGLE
Sr_{15}	7 A	AXIMINSTER; NORKA; NORMANDIE
Sr_{22}	7 A	T. MONOCOCCUM; T. BOEOTICUM
Sr_{14}	1 B	GIORGIO 302; KHAPSTEIN; KHAPLI (T. Dicoccum)
Sr_{9a}	2 B	RED EGYPTIAN
Sr_{9b}	2 B	KENYA 117A; FRONTANA; MAGNIFIC G; PITIC 6
Sr_{9d}	2 B	HOPE; RENOWN; SELKIRK
Sr_{16}	2 B	THATCHER; RELIANCE
Sr_{19}	2 B	MARQUIS
Sr_{20}	2 B	RELIANCE; MARQUIS
Sr_{28}	2 B	KOTA
Sr_{12}	3 B	MARQUIS; THATCHER
Sr_{7a}	4 B	KENYA 117A; KENYA FARMER; KHAPSTEIN
Sr_{7b}	4 B	SPICA; RENOWN; SELKIRK
Sr_{11}	6 B	KENYA FARMER; GABO; LEE; SONORA 64; YALTA
Sr_{17}	7 B	HOPE; RENOWN; SPICA
Sr_{18}	1 D	HOPE
Sr_{6}	2 D	KENYA 58; AFRICA 43; SELKIRK; FKN
Sr_{24}	3 DL	AGENT; BLUEBOY II
Sr_{5}	6 D	THATCHER; RELIANCE
Sr_{25}	7 DL	AGATHA

To genes mentioned above (Table IV) we may add those not yet classified and localized, present in Italian varieties (Elia, Est Mottin, Mont Calme) (Zitelli and Vallega [6, 18]) in durum wheats from Spain (Duranzio Rijo Glabro, Obispado Jerez, *T. durum* Korn etc.) (Salazar et al. [19]) in some Egyptian wheats (Gaza, Beladi 116 e Egipto), and in Ethiopian wheats (St. 464) (Zitelli [20]).

TABLE V. REACTION OF 102 DIFFERENT FORMS OF *T. Monococcum* TO *Puccinia graminis* AND *Erysiphe graminis tritici.*

No. of forms	No. of forms resistant to:			
	Races of *Puccinia graminis tritici*		Population of *Erysiphe graminis tritici*	*Puccinia graminis tritici* + *Erysiphe graminis tritici*
	14-Italy II	116		
102	49	73	87	40

Also *T. monococcum* species (Vallega [21], unpublished) turned out to be a very rich source of genes for resistance, useful for the group of races of *P. graminis* present in Italy, and especially for the biotypes of race 14. (Table V).

For leaf rust, 25 factors have been identified, among which 20 have also been localized (Table VI). Interesting factors, although not yet identified and localized, are present in Elia, Est Mottin, Rieti, Apulia, (Zitelli and Vallega [18]), especially in lines Giorgio, and Gerardo (Zitelli and Vallega [6]; Zitelli [20]). In this group of wheats there are genes that promote resistance to all races of *P. recondita* present in Italy (race 77 included) (Cariello et al. [22]), as well as factors favouring non-specific resistance (Vallega and Zitelli [23]).

Nine genes determining resistance to mildew are known; they are localized in six chromosomes. Considering, however, the parasite variability, they are likely to be insufficient to ensure a stable resistance. In Italy the only effective gene is Pm_2, present in Wisconsin Sel. C.I. 12632 (derived from *T. timopheevi)* (Zitelli [24]) because of the fact that, in the Italian parasite population, there exist, although sporadically and to a minimum degree, virulent genes capable of attacking Pm_4 (present in Khapli and Yuma). There is, consequently, a need to find other genes for resistance, perhaps also in related species, or of obtaining them artificially, through mutagenesis.

In the case of *Septoria tritici,* no source for resistance has yet been found in *T. aestivum* and *T. durum.* This seems due to the extreme variability of the parasite and to the different manifestations of the disease (Scharen and Krupinsky [25]).

Actually, rather than towards specific genes for resistance, the search is directed towards tolerant varieties (Brönnimann [26]). It is likely that *Septoria* has become a serious problem in recent times because of the repeated cultivation of wheat in the same field as well as in relation to the use of dwarf varieties (possessing Norin 10 factors).

TABLE VI. GENES FOR LEAF RUST RESISTANCE *(from McIntosh* [10, 11])

Genes.	Chromosome.	Varieties
Lr_{10}	1 A	EXCHANGE; GABO; LEE; SELKIRK
Lr_{11}	2 A	HUSSAR
Lr_{12}	4 A	EXCHANGE
Lr_{16}	4 A	EXCHANGE; ETOILE DE CHOISY
Lr_{25}	4 A	TRANSEC
Lr_{20}	7 A	AXMINSTER; NORMANDIE; NORKA
Lr_{1}	1 B	CENTENARIO; MALAKOFF; SONORA 64
Lr_{2a}	1 B	WEBSTER; FESTIGUAY
Lr_{2b}	1 B	CARINA
Lr_{2c}	1 B	BREVIT; LOROS
Lr_{23}	2 B	LEE
Lr_{3}	6 B	DEMOCRAT; BEZOSTAJA 1
Lr_{9}	6 B	TRANSFER
Lr_{14a}	7 B	SELKIRK; RENOWN; SPICA
Lr_{14b}	7 B	THATCHER
Lr_{14ab}	7 B	THATCHER
Lr_{21}	1 D	TETRA; CANTHATCH (Ae. Squarrosa v. Meyeri)
Lr_{15}	2 D	KENYA W 1483
Lr_{22}	2 D	TETRA; CANTHATCH (Ae. Squarrosa v. Strangulata)
Lr_{24}	3 D	BLUEBOY
Lr_{19}	7 D	AGATHA (Agropyron Elongatum translocation 4)

Our observations on Italian varieties of bread wheats, characterized by short height (Mara, Victor, Acciaio) (Zitelli and Mariani [27]), produced by dwarfism factors different from those of Norin 10, allow us to conclude that reduced height does not necessarily mean greater susceptibility to *Septoria*. The varieties mentioned, in fact, are less than 80 cm high, but do not exhibit the poor resistance to *Septoria* that is typical of the material derived from Norin 10.

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