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A GENE-FOR-GENE RELATIONSHIP IN THE *TRITICUM-USTILAGO* SYSTEM, AND SOME REMARKS ON HOST-PATHOGEN COMBINATIONS IN GENERAL

Een gen-om-gen verband bij tarwe – stuifbrand en enige opmerkingen over gastheer-pathogeen-combinaties in het algemeen

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As a result of a series of investigations on the genetics of the resistance of flax to flaxrust (*Melampsora lini*) carried out from 1940 onwards Flor (1956, 1959) put forward the hypothesis that for each specific locus determining resistance and susceptibility in the host there is a specific and related locus in the pathogen which determines pathogenicity. He stated (1959, p. 137): "The genes in the host that condition resistance can be identified only by their interaction with specific cultures of the parasite; the genes in the parasite that condition pathogenicity can be identified only by their interaction with specific varieties of the host". Bij crossing experiments Flor gave substantial evidence for the correctness of his view. This relationship was named a gene-for-gene relationship. Toxopeus (1956) making use of the data of Black, Mastenbroek, Mills and Peterson (see for references Toxopeus l.c.) suggests that in the *Solanum-Phytophthora* system a similar relationship occurs. In a recent publication Person (1959) gives an analysis of the work carried out on both host-pathogen systems and explains the characteristics of the gene-for-gene relationship. He comes to the conclusion that such a relationship should be the rule in host-pathogen systems. Quite recently a third case has been mentioned by Metzger & Trione (1962) regarding the relationship between wheat and bunt (*Tilletia*).

The present author working with loose smut (*Ustilago tritici*) of wheat suggested already in 1944 what Flor has called a gene-for-gene relationship. Since the published report of this investigation has remained unnoticed probably because of the war, some of the data will be reviewed here. For further details see the original publication. In the course of the investigations on resistance and susceptibility 6 physiologic races could be differentiated on 9 groups of wheat varieties. For convenience the term "physiologic race" is used, though not quite correct in the sense it is generally applied. However, the strains derived from mass spore isolations each from one host variety, proved to be remarkably constant and behaved like physiologic races.

Two types of resistance mechanism were recognized. The first type determines whether the plant is susceptible (shows symptoms) or resistant (no symptoms). The second type – superimposed on the first – determines whether either normal loose smut symptoms will develop, or abnormal symptoms without spore formation. The abnormal reaction of wheat to loose smut consists of dwarfing in the seedling stage, in severe cases leading to the death of the seedling; in less severe

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cases the plants recover and develop healthy ears without any loose smut symptoms. Recovered plants, however, remain dwarfed or are at least smaller than normal ones. The abnormal reaction was ascribed by the author to hypersensitivity, but as shown by MANTLE (1961) after an anatomical examination, this term is inadequate for the observed phenomenon. MANTLE named it incompatibility, which term will be used in this publication. Since, however, no smut spores are formed, it can be considered as another type of resistance. For the sake of brevity, only the first type of resistance will be referred to as resistance.

The results of all possible inoculations of the 9 variety groups with the 6 physiologic races are shown in table 1, which is copied from table 13 of the 1944 publication but with amended symbols for resistance and virulence. In this table a circle means resistance and a square susceptibility (first type of resistance mechanism); an open square refers to incompatibility and a hadched one to compatibility, the latter being the normal loose smut development (second type of resistance mechanism).

TABLE 1. Interactions of 9 groups of varieties with 6 physiologic races. Circle: resistant; open square: susceptible and incompatible (abnormal symptoms); hatched square: susceptible and compatible (normal loose smut symptoms). A, B, C factors for resistance; M, N factors for incompatibity; a, b, c and m, n factors for virulence.

	Physiologic race					1	2	3	4	5	6
				Virulence expressed by:				a	a		
										b	b
										c	
Variety group	Resistance/ incompatibility expressed by:						m		m	m	m
						n	n	n	n		n
V				M		□	▨	□	▨	▨	▨
VII					N	▨	▨	▨	▨	□	▨
VI				M	N	□	▨	□	▨	□	▨
IX	A			M	(N)[1]	○	○	□	▨	○	○
VIII	A				(N)	○	○	▨	▨	○	○
IV		B		(M)[1]		○	○	○	○	▨	▨
III		B		(M)	N	○	○	○	○	□	▨
II			C	(M)	N	○	○	○	○	□	○
I	A	B		(M)	(N)	○	○	○	○	○	○

[1] available data do not permit a conclusion about presence or absence of factor between brackets

To explain the results of the wheat loose smut interaction observed, it was assumed in the original publication that two sets of specific factors for resistance in the host interfere with two complementary sets of factors for virulence (pathogenicity) in the pathogen. In a similar way two sets of specific factors for incompatibility were assumed to interfere with two sets of corresponding factors for virulence in the pathogen.

In this way the interactions of 8 groups of wheat varieties with 6 physiologic races could be demonstrated. For the reactions of one group of varieties a third factor for resistance corresponding with a third factor for virulence had to be taken into account.

In contrast with the original table, the letters designating the genes have here been brought into agreement with the notation of PERSON (1959). For resistance in the host the factors A, B and C are corresponding with the factors a, b and c for virulence in the pathogen. The resistance in A can only be overcome by a physiologic race of the pathogen possessing the a factor for virulence. The same holds for the factors B and C in the host and b and c respectively in the pathogen.

Factors giving incompatibility are indicated by M and N. Races possessing m or n can overcome the incompatibility induced by M or N, so that the plant develops normal smut symptoms. In those cases which did not permit a conclusion as regards the presence or absence of a factor, the factor has been placed between brackets.

TABLE 2. Hypothetical scheme of host-pathogen interactions based on gene-for-gene relationships involving four sets of complementary genes in host and pathogen.
Circle: resistant; open square: susceptible and incompatible (abnormal symptoms); hatched square: susceptible and compatible (normal loose smut). Interactions of the 8 variety groups and the 6 physiologic races actually observed by the author are shown in bold type.

Variety groups	Author's numbers[1]	Physiologic races	P 1 2 3 4	5 6 7 8	9 10 11 12	13 14 15 16
		Author's numbers	1 2	3 4	6 5	
		Virulence expressed by:		a a a a	b b b b	a a a a b b b b
		Resistance/ incompatibility expressed by:	m m n n	m m n n	m m n n	m m n n
H 1			▨ ▨ ▨ ▨	▨ ▨ ▨ ▨	▨ ▨ ▨ ▨	▨ ▨ ▨ ▨
2	V	M	□ ▨ **□** **▨**	□ ▨ **□** **▨**	□ **▨** □ **▨**	□ ▨ □ ▨
3	VII	N	□ □ **▨** **▨**	□ □ **▨** **▨**	□ **□** □ **▨**	□ □ ▨ ▨
4	VI	M N	□ □ **□** **▨**	□ □ **□** **▨**	□ **□** □ **▨**	□ □ □ ▨
5	(VIII)[2]	A	○ ○ ○ ○	▨ ▨ ▨ ▨	○ ○ ○ ○	▨ ▨ ▨ ▨
6	IX	A M	○ ○ **○** **○**	□ ▨ **□** **▨**	○ **○** ○ **○**	□ ▨ □ ▨
7	VIII	A N	○ ○ **○** **○**	□ □ **▨** **▨**	○ **○** ○ **○**	□ □ ▨ ▨
8	(IX)[2]	A M N	○ ○ ○ ○	□ □ □ ▨	○ ○ ○ ○	□ □ □ ▨
9	(IV)[2]	B	○ ○ ○ ○	○ ○ ○ ○	▨ ▨ ▨ ▨	▨ ▨ ▨ ▨
10	IV	B M	○ ○ **○** **○**	○ ○ **○** **○**	□ **▨** □ **▨**	□ ▨ □ ▨
11	III	B N	○ ○ **○** **○**	○ ○ **○** **○**	□ **□** ▨ **▨**	□ □ ▨ ▨
12	(III)[2]	B M N	○ ○ ○ ○	○ ○ ○ ○	□ □ □ ▨	□ □ □ ▨
13	I	A B	○ ○ **○** **○**	○ ○ **○** **○**	○ **○** ○ **○**	▨ ▨ ▨ ▨
14	(I)[2]	A B M	○ ○ ○ ○	○ ○ ○ ○	○ ○ ○ ○	□ ▨ □ ▨
15	(I)[2]	A B N	○ ○ ○ ○	○ ○ ○ ○	○ ○ ○ ○	□ □ ▨ ▨
16	(I)[2]	A B M N	○ ○ ○ ○	○ ○ ○ ○	○ ○ ○ ○	□ □ □ ▨

[1] group II has been omitted

[2] alternative place of variety group in scheme

In table 2 the interactions of the 16 possible variety groups of the host with the 16 possible physiologic races of the pathogen are given, assuming 4 independent factors for resistance/incompatibility and 4 independent factors for virulence. The third factor for resistance C has been omitted in this table. The interactions of the groups and races determined in the author's investigations are printed in bold type.

To test the correctness of the assumption that specific genes for resistance and incompatibility correspond with specific genes for virulence crossings were made. All the seed of the crosses, however, was lost during the last year of the war, and after the war the work has not been resumed.

The interactions as shown in tables 1 and 2, however, make it probable that the *Triticum-Ustilago* system fits the conditions put forward by PERSON (1959) for a gene-for-gene relationship.

Since preparing this article a publication by PERSON, SAMBORSKI & ROHRINGER (1962) has appeared in which special attention is given to the limits within which gene-for-gene relationships are likely to occur, and in which a definition of the concept is proposed. In connection with this article and also the view put forward by PERSON (1959) that a gene-for-gene relationship should be the rule in host-pathogen systems it seems appropriate to make some comments on the applicability of the concept to true host-parasite systems. In this connection a distinction must be made between systems in which the pathogen is biotrophic and those in which it is perthotrophic.

The biotrophic pathogens (corresponding mainly with the obligate parasites) are wholly dependent on the living plant. They include, for example, the rusts, powdery and downy mildews, *Phytophthora infestans*, most smuts and *Synchytrium*. Outside the living host they can only persist in the form of resting spores. Most pathogens of this category are highly specialized and the host range of a physiologic race is often confined to a small group of varieties or related species. Survival is likely to occur mainly by specific mutations for virulence which can overcome specific factors for resistance in the host. Gene-for-gene relationships may therefore be expected to develop frequently. All established relationships (*Linum-Melampsora*, *Solanum-Phytophthora*, *Triticum-Tilletia*) and presumed relationships (*Triticum-Ustilago*) fall within this group.

In the case of perthotrophic pathogens (corresponding mainly with the facultative parasites) the situation is quite different. They kill the host and live from the dead tissue. Some of them, such as species of *Pythium* and *Corticium*, are soil-inhabiting parasites according to GARRET's classification and can even live on organic material in the soil in the absence of the host and in competition with other soil organisms. Others, represented by some of the root-inhabiting parasites as for instance *Ophiobolus* and *Fomes* species, also persist as saprophytes, but only on the host tissues previously killed. In their saprophytic stages and also when growing along the roots (ectotrophic growth habit) they have also to compete with soil organisms. In many cases specialization is low and generally speaking there seems no urgent need for enlargement of the host range by mutation to greater virulence. Ability to persist saprophytically may be of much greater importance in the struggle for survival, and gene-for-gene relationships may be expected therefore to occur more rarely. As suggested by PERSON et al. (1962), such might be the case with *Avena* and *Ophiobolus graminis* f. *avenae*.

Since in the case of perthotrophic pathogens survival may be expected to be governed to a greater extent by factors not of a gene-for-gene nature, host resistance mechanisms against such perthotrophic pathogens may similarly involve specific gene-for-gene relationships more rarely.

It may be assumed therefore that non-specific resistance mechanisms are more commonly acting in host-perthotrophic pathogen systems and specific resistance mechanisms in host-biotrophic pathogen systems. However, in the latter case non-specific defence mechanisms also occur. The so-called field resistance of the potato against *Phytophthora* is such a non-specific mechanism counteracting all races simultaneously.

The above interpretation, if correct, limits the validity of PERSON's statement (l.c.) that a gene-for-gene relationship should be the rule in host-pathogen systems.

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SUMMARY

In the *Triticum-Ustilago* system a gene-for-gene relationship presumably exists. Two sets of resistance factors and two sets of incompatibility factors in the host, corresponding to four sets of complementary factors for virulence in the pathogen, can explain the interactions of 8 variety groups of the host with 6 physiologic races of the pathogen.

Some comments are made on the applicability of the gene-for-gene concept in systems involving either a biotrophic or a perthotrophic pathogen as one of the partners.

SAMENVATTING

Bij de combinatie tarwe – stuifbrand bestaat vermoedelijk een gen-om-gen verband. Twee paar resistentie- en twee paar incompatibiliteitsfactoren in de gastheer, corresponderende met vier paar complementaire virulentiefactoren in het pathogeen, kunnen de interacties verklaren van 8 rassengroepen van de gastheer met 6 fysio's van het pathogeen.

Naar aanleiding van de publikaties van PERSON (1959) en PERSON et al. (1962) worden enkele opmerkingen gemaakt betreffende de toepasbaarheid van het gen-om-gen begrip in combinaties waarbij hetzij een biotroof hetzij een perthotroof pathogeen een van de partners is.

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