GENES FOR AND MOLECULAR MARKERS LINKED WITH RESISTANCE TO *PHYTOPHTHORA FRAGARIAE* IN STRAWBERRY

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Summary

A gene-for-gene model is presented which explains interactions between cultivars of strawberry and races of *Phytophthora fragariae* var. *fragariae*, the causal agent of red core (red stele) root rot. The model allows the constitution of a universal differential set of strawberry genotypes and the characterizing of fungal isolates into races, the genotyping of strawberry cultivars and selections in a breeding programme, and facilitates the search for linked molecular markers for more efficient selection for resistance.

1. Introduction

Phytophthora fragariae var. *fragariae* (Hickman, 1940; Wilcox *et al.*, 1993) is the causal agent of red stele (red core) root rot in strawberry (*Fragaria x ananassa*). It is widely assumed that resistance to this soil-borne fungus is inherited polygenically (Stembridge and Scott, 1959; Scott *et al.*, 1984). However, the race specificity (Converse, 1970; Kennedy and Duncan, 1993; Nickerson and Murray, 1993) and the observed Mendelian segregation of resistance (Van de Weg *et al.*, 1989) suggest that genotypes of strawberry and races of *P. fragariae* exhibit a gene-for-gene (GFG) relationship as first described by Flor (1956) for flax and flax rust (*Melampsora lini*). The published reports on cultivar-race interaction data at first appeared too inconsistent (Milholland, 1994; Van de Weg, 1989) to derive GFG patterns. However, a number of inconsistencies are due to differences in the evaluation of incompletely expressed resistance, to interchanges of cultivars which were incorrectly presumed to have the same resistance, and to the existence of different genotypes under the same cultivar name (Van de Weg *et al.*, 1997). Data from which the inconsistencies were removed (Van de Weg *et al.*, 1997), fit very well in a recently developed GFG model (Van de Weg, 1997a). Here, this model and its repercusions are discussed.

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2. The GFG concept

The GFG hypothesis (Flor, 1956) presumes that for each resistance factor in the host, there is a corresponding avirulence factor in the pathogen (Newton and Andrivon, 1995). Recently, the molecular interpretation of GFG models has been postulated. The product of the resistance allele is supposed to recognize the product of the corresponding avirulence allele, which initiates the resistance response (Keen, 1990). In contrast, the product of the virulence allele will not be recognized by the product of the resistance allele, resulting in virulence of the pathogen and in susceptibility of the host (Newton and Andrivon, 1995). Thus, resistance occurs if a cultivar carries at least one resistance allele for which the pathogen carries the corresponding avirulence allele. Susceptibility requires either the absence of any resistance (R-) allele, or the avoidance of each R-allele in the host by the absence of the matching avirulence allele in the pathogen.

3. Validity of the GFG-model

The proposed GFG model (Table 1) fits to earlier data (Kennedy and Duncan, 1988, 1993; Kennedy *et al.*, 1986; Law and Milholland, 1992; Maas *et al.*, 1989; Milholland *et al.*, 1989; Scheewe, 1994) on the resistance and virulence of UK, USA and German strawberry differentials and fungal isolates (Van de Weg, 1997a). Moreover, inheritance studies confirmed the expected monogenicity of resistance factor 2 (Van de Weg, 1997b). The relative gene was designated *Rpf2* following Søgaard and Wettstein-Knowles (1987).

Recent research on cultivar-race interactions delivered the existence of three additional resistance factors (R6-R8), of which the monogenicity of R6 has been established in inheritance studies. Consequently, the GFG-model of Table 1 has yet to be extended. An updated model will be published as soon as the relative research has been completed.

4. Composition of an universal set of differential cultivars

Differential sets of strawberry genotypes are needed to identify races of the fungus. The most efficient set consists of host genotypes each possessing a single, unique resistance factor and together comprising all known R-factors (Person, 1959; Flor, 1971). A universally susceptible cultivar should be included to identify isolates lacking any specific avirulence factors (race Avr0). The set could thus consist of genotypes such as: 'Blakemore' (no resistance), Md683 (R1), 'Sparkle' (*Rpf2*), CPRO-D3 (R3), 'Yaquina B' (R5). Differentials for R4, R6, R7, and R8 are currently being developed at CPRO-DLO. Differential CPRO-D3 originates from the cross 'Perle de Prague' x 'Senga Sengana' and will be available from autumn 1996.

5. Genotyping of breeding selections

In various breeding programmes for resistance to *P. fragariae* three resistances are important: R1, *Rpf2*, and R3. These allow the identification of 8 different genotypes, which each show a unique pattern of reactions when tested against isolates A8, NS2,

NS3, and NS4 (Table 2). Testing with these isolates thus allow the genotyping of cultivars, crossing parents, and advanced selections.

6. Molecular markers

The GFG model allows the identification of molecular markers for resistance as progenies segregating for the genes of interest can be created and the individuals of these progenies can be genotyped. Recently, molecular markers were identified for R1 using the PCR/BSA technique (Haymes *et al.*, 1997a,b). The availability of these markers open a completely new methodological approach in strawberry breeding. Plant material has recently been developed for the identification of molecular markers for *Rpf2*, R4, R5, and R6.

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Table 1. A gene-for-gene model explaining the interactions between cultivars of strawberry and isolates of *Phytophthora fragariae* var. *fragariae* by five pairs of interacting resistance and avirulence factors. The model is according to Van de Weg (1997a), to which data on CPRO-D3 were added.

Strawberry genotypes and their resistance factors		American (A) and Canadian (NS) isolates and their proposed avirulence factors									
		A1	A2[1]	A3	A6	A7[2]	A8	A9	A10	NS2	NS4
		1	1	1	1	.	.	1	1	1	.
		.	2	.	.	2	.	2	2	.	.
		3	3	.	3	.	3	.	.	.	.
		4	.	4	.	4	4	4	.	.	4
		5	5	5	5	5	5	5	5	5	5
Blakemore	0	+	+	+	+	+	+	+	+	+	+
Md683	1	-	-	-	-	+	+	-	-	-	+
Sparkle	2	+	-	+	+	-	+	-	-	+	+
CPRO-D3	3	-	-	+	-	+	-	+	+	+	+
Del Norte	4	-	+	-	+	-	-	-	+	+	-
Yaquina B	5	-	-	-	-	-	-	-	-	-	-
Stelemaster	1.2	-	-	-	-	-	+	-	-	-	+
Perle de Prague	1.3	-	-	-	-	+	-	-	-	-	+
Aberdeen	2.3	-	-	+	-	-	-	-	-	+	+

[1, 2] Isolates having identical interactions; [1]: A2; [2]: NS3.

Table 2. Resistances of eight theoretical strawberry genotypes to four isolates (A8, NS2, NS3, NS4) of *P. fragariae* var. *fragariae* based upon the GFG model (Table 1). Genotypes are characterised by the resistance factors they possess.

Genotype	Isolates and their avirulence factors			
	NS2	NS3	A8	NS4
	1.5	2.4.5	3.4.5	4.5
0	+	+	+	+
1	-	+	+	+
2	+	-	+	+
3	+	+	-	+
1.2	-	-	+	+
1. 3	-	+	-	+
2.3	+	-	-	+
1.2.3	-	-	-	+