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Race-specific aspects of polygenic resistance of barley to leaf rust, Puccinia hordei

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Abstract

Partial resistance of barley to leaf rust, *Puccinia hordei*, is characterized by a reduced rate of epidemic development in spite of a susceptible infection type. Barley cultivars vary greatly for partial resistance and its components. In a test for interaction between host cultivars and pathogen isolates most variation was of a horizontal nature. However, in the combination between 'Julia' and the rust isolate 18, a differential interaction (vertical effect) occured; 'Julia' had lost a small part of its partial resistance. The same interaction was found for latent period (LP), the most important component of partial resistance. 'Julia' showed a shortened LP for isolate 18. Genetic analyses revealed, that 'Julia' carries a polygene for longer LP not present in the other cultivars. The effect of this polygene appears to be 'broken' by isolate 18 indicative for a gene-for-isolate relation, and even for a gene-for-gene relation.

Introduction

Vertical or race-specific resistance is characterized by differential interactions between host and pathogen, horizontal or race non-specific resistance by the absence of such interactions (Van der Plank, 1968, 1975a). Van der Plank (1975b) stated: 'Characteristically, horizontal resistance (HR) slows epidemics down. Sporulation is less abundant, or fewer spores infect, or the time taken from infection to sporulation is increased, or these effects occur together. And the effects derive, I believe, from a genetic basis distinct from that of vertical resistance (VR)'. He also concluded that the definition of HR rules out the posibility of any gene-for-gene relation (Van der Plank, 1975a, p. 167).

Parlevliet and Zadoks (1977), accepting Van der Plank's definition of HR and VR, did not agree with his ideas about the genetic basis of HR. They showed, through simulation studies, that polygenic resistances operating on a gene-for-gene basis with polygenes in the pathogen, could be race non-specific or horizontal in nature. They assumed that most true resistance genes operate on a gene-for-gene basis with genes in the pathogen. Polygenic resistances of a horizontal nature are supposed to be stable because many genes and not because other genes are involved.

The purpose of this paper is to show that polygenes indeed can behave as major, race-specific or vertical resistance genes do.

The barley-leaf rust relationship; partial resistance

The partial resistance of barley to leaf rust, *Puccinia hordei* Otth, is a typical example of resistance considered horizontal or race non-specific by Van der Plank (1968, 1975a, b). The partial resistance to leaf rust is characterized by a reduced rate of epidemic development in spite of a susceptible infection type (Parlevliet and Van Ommeren, 1975). Barley cultivars vary in partial resistance largely as a result of differences in its components: infection frequency, latent period[1], sporulation rate and infectious period (Parlevliet, 1975; Neervoort and Parlevliet, 1978). Parlevliet and Van Ommeren (1975) measured the partial resistance of 16 spring barley cultivars. To avoid interference between cultivars the plots with the various cultivars were isolated from one another by at least 30 m of winter wheat (eight plots of 3.0 × 4.0 m of barley per ha of winter wheat). Large differences in partial resistance were observed. Table 1 shows six of these cultivars representing the known range in partial resistance.

Table 1. Epidemic build-up of leaf rust, *Puccinia hordei*, in isolated field plots seven weeks after inoculation at stage 6–7 of the Feekes scale, and latent period in the young flag leaves of six spring barley cultivars (adapted from Parlevliet, 1976a).

		Cultivar					
		L94	L98	Zephyr	Berac	Julia	Vada
Number of uredo sori per tiller in:	1973	2800	1000	510	–	17	1.1
	1974	750	700	40	1.9	1.5	0.5
Latent period (days)		7.8	9.4	11.1	12.3	12.7	14.8

Tabel 1. Epidemie-opbouw van dwergroest, Puccinia hordei, in geïsoleerde veldjes zeven weken na inoculatie in stadium 6–7 van de Feeks schaal, en latentieperiode in het jonge vlagblad van zes zomergerstrassen (aangepast naar Parlevliet, 1976a).

When the partial resistance in barley to leaf rust is of a horizontal nature there should be no differential interaction when host cultivars are tested against pathogen isolates (Van der Plank, 1968, 1975a). To study this, the partial resistance of three cultivars was measured for five leaf rust isolates. The plots were separated by winter rape to prevent cross contamination and cultivar interference (Parlevliet, 1977). Fairly resistant cultivars were chosen as it was felt that possible deviations from a horizontal pattern would be easier to measure among resistant than among susceptible cultivars. Table 2 shows the disease severities. The horizontal aspects dominate; 'Berac' is least resistant to each isolate. The pathogenicity of the isolates decreases from 11–1 to 24. Only 'Julia' × isolate 18 forms a clear exception. This differential interaction indicates vertical effects (vertical resistance and vertical pathogenicity). Most variations in resistance and pathogenicity, however, are horizontal. This is even more so when one takes into account that susceptible cultivars like 'L94' or 'L98' (Table 1), when included in this experiment, would have scored

1 Although latency period is the correct term, latent period is used here to harmonize with the general use in the literature.

Table 2. Disease severity just prior to maturation expressed in percentage leaf area affected of three barley cultivars infected by five isolates of *Puccinia hordei* (Parlevliet, 1977).

Cultivar	Isolate				
	11–1	18	1–2	22	24
Berac	8.1	6.7	3.1	5.0	0.9
Julia	4.5	12.1[1]	1.8	1.1	0.6
Vada	0.8	0.5	0.6	0.22	0.06

[1] In absence of interaction ca. 3% (calculated when additively is assumed between cultivar and isolate effects)

Tabel 2. Mate van aantasting vlak voor afrijping uitgedrukt in percentage aangetast bladoppervlak, van drie gerstrassen voor vijf isolaten van Puccinia hordei (Parlevliet, 1977).

over 40% leaf area affected for all isolates, isolate 24 inclusive. Compared to the total variance in resistance this differential interaction is a minor, but significant effect. Thus, the pathogen population carries the genetic potential to break down the partial resistance in small steps.

The barley-leaf rust relationship; latent period

Partial resistance of barley to leaf rust is largely governed by one or more of several components; infection frequency, latent period, sporulation rate and infectious period. Parlevliet and Van Ommeren (1975) and Neervoort and Parlevliet (1978) showed that the latent period (LP) is the crucial component of partial resistance in this host-pathogen relationship. The correlation between partial resistance in the field and LP measured in the young flag leaves was very high ($r = -0.92$), (Parlevliet and Van Ommeren, 1975).

Because LP was strongly correlated with partial resistance in the field and could be measured with much accuracy than the other components (Neervoort and Parlevliet, 1978; Parlevliet, 1977) it was used for more detailed studies, a genetic analysis and an analysis of the relation between host cultivars and pathogen isolates.

The genetic analysis of LP measured on the flag leaves concerned seven cultivars, including 'L94', 'Julia' and 'Vada' (Parlevliet, 1976b, 1978). The inheritance of host effects on LP in the seven cultivars is supposed to be governed by seven loci. Table 3 shows the assumed genotypes of 'L94', 'Julia' and 'Vada'. Each + allele increases the LP somewhat. 'Julia' and 'Vada' are thought to carry five and six minor genes for a longer LP (+ alleles) resp. of which four are the same. 'Julia' has one minor gene not carried by 'Vada' nor by 'L94', the one on locus 5. The genetic analyses were done with leaf rust isolate 1–2, also used in the host-pathogen interaction studies (Table 2 and 4).

In two tests for interaction between host cultivars and pathogen isolates the LP on young flag leaves was measured for several host-pathogen combinations (Parlevliet, 1976a and 1977). Table 4 shows the results for four cultivars and five isolates. Isolates 1–2, 12 and 15 gave similar LP's on all cultivars. They were taken together. Isolates 11–1 and 18 caused LP's slightly longer than the means of those of the other three.

Table 3. The genetic constitution of three barley cultivars on seven loci governing latent period for leaf rust, *Puccinia hordei*, isolate 1–2, in the adult plant stage (adapted from Parlevliet, 1978).

Cultivar	Locus						
	1	2	3	4	5	6	7
L94	– –	– –	– –	– –	– –	– –	– –
Julia	+ +	+ +	+ +	+ +	+ +	– –	– –
Vada	+ +	+ +	+ +	+ +	– –	+ +	+ +

Tabel 3. De genetische samenstelling van drie gerstrassen op zeven loci voor latentieperiode voor dwergroest, Puccinia hordei, isolaat 1–2, in het volwassen-plantstadium (aangepast naar Parlevliet, 1978).

Table 4. Latent periods in days in the young flag leaves of four barley cultivars inoculated with five isolates of *Puccinia hordei* (adapted from Parlevliet, 1976a).

Cultivar	Isolate		
	11–1	18	mean of three similar isolates[1]
L94	8.1[ab]	8.3[b]	7.8[a] [2]
Berac	14.0[d]	13.9[d]	12.3[c]
Julia	15.1[e]	12.8[c d] [3]	12.7[c d]
Vada	17.2[f]	18.6[f]	14.8[e]

[1] The isolates were 1–2, 12 and 15.
[2] Latent periods carrying different letters are significantly different according to Duncan's multiple range test (P = 0.05).
[3] In absence of interaction ca. 15 days (see note 1, Table 2).

Tabel 4. Latentieperiode in dagen in de jonge vlagbladen van vier gerstrassen geïnoculeerd met vijf isolaten van Puccinia hordei (aangepast naar Parlevliet, 1976a).

The 'Julia'-isolate 18 combination gave a LP significantly shorter than expected on the basis of no interaction. This interaction tallies very well with that found for partial resistance in the field (Table 2). The decreased partial resistance of 'Julia' with respect to isolate 18 apparently resulted from the shorter LP caused by that isolate.

The barley-leaf relationship; race specific aspects

The shortened LP of 'Julia' for isolate 18 suggests taht isolate 18 can neutralize the effects of the minor gene on locus 5 (Table 3) but not of those on the other loci. The LP's of 'L94' and 'Vada' for isolate 18 were not shortened relative to those for 11–1. This in fact is a gene-for-isolate relation and it is tempting to postulate a virulence gene carried by isolate 18 able to neutralize only the effects of locus 5 and this would be a true gene-for-gene relationship.

This situation, considering the minor genes individually, closely resembles that well known from the race-specific or vertical major genes, where the effects of a resistance gene depends on the isolate used (Flor, 1971; Person and Sidhu, 1971; Day, 1974) With major genes for resistance and pathogenicity races of the pathogen can be clearly distinguished. With minor genes involved the race-specific effects are small, so small, that it is hard to classify isolates on the basis of such effects. The concept 'race' is difficult to apply here. Then the five isolates of Table 2 would have to be classifield as two races, isolate 18 being one race, the other four together being the other race, to be distinguished on 'Julia'. However, this is of no use as the differences between the four isolates, to be classified as one race, are of the same order as the difference between isolate 18, the other race, and for instance isolate 11–1 or 1–2. This quantitative variation results from polygenic inheritance of resistance and from the probably polygenic inheritance of the corresponding pathogenicity. The small interaction effects are hard to detect within the large quantitative variation present in both host and pathogen populations. The overall impression is of a horizontal resistance, with absence of race-specific aspects. A more detailed study may reveal small vertical, race-specific effects, so small that in many trials such effects can not be discerned from the trial error.

Another consequence of the conclusion that the effect of a polygene depends on the isolate used is that a genetic analysis as shown in Table 3 is valid only for the isolate used. Minor resistance genes can only be detected when the isolate used for testing carries the corresponding avirulence genes.

Polygenic resistance like the one discussed here is often considered to be stable (Van der Plank, 1968, 1975a, 1975b; Ullrich, 1976). Parlevliet and Zadoks (1977) conclude that the durability of polygenic resistances is derived from the difficulty the pathogen population has to adapt on several loci. Incorporation of one virulence gene to break resistance is far easier for the pathogen than incorporation of several minor virulence genes to erode the pertial resistance. This situation resembles that with fungicides. Development of resistance to multi-site inhibitors is at best rare, but the development of resistance to systemic fungicides, which are mono-site or site-specific inhibitors, has been reported in many instances (Dekker, 1976).

Samenvatting

Fysio-specifieke aspecten van polygene resistentie van gerst tegen dwergroest, Puccinia hordei

Partiële resistentie van gerst voor dwergroest, *Puccinia hordei*, is gekenmerkt door een vertraagde epidemie-opbouw ondanks een vatbaar infectietype. Gerstrassen variëren sterk in partiële resistentie en haar componenten. In een toets ter bestudering van de interactie tussen waardplant en pathogeenisolaat bleek de meeste variatie horizontaal van aard te zijn. In de combinatie van 'Julia' met isolaat 18 werd echter een differentiële interactie waargenomen; 'Julia' had een klein deel van zijn partiële resistentie verloren. Dezelfde interactie werd waargenomen voor de belangrijkste component van partiële resistentie, de latentieperiode (LP); 'Julia' had een iets verkorte LP voor isolaat 18. Genetische analyses toonden aan, dat 'Julia' een polygen voor langere LP bevat; dit gen is niet aanwezig in de andere bestudeerde rassen. Er wordt verondersteld dat het effect van dit polygen door isolaat 18 is 'doorbroken'. Dit wijst op een gen-om-isolaat en zelfs op een gen-om-gen-relatie.

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