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Resistance of some barley cultivars to leaf rust, Puccinia hordei; polygenic, partial resistance hidden by monogenic hypersensitivity

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Abstract

Three cultivars, all carrying the Pa7 gene for low infection type were crossed with 'L94', a cultivar assumed to carry no genes for partial resistance. The latent period (LP), the most important component determining partial resistance, was measured on 111 F_2 plants not carrying the Pa7 gene and on four cultivars representing the known range in LP. Of 20 F_3 lines the LP was evaluated, too. The F_2 showed a continuous segregation for LP from nearly as short as 'L94' to as long as 'Vada'. This was substantiated by the F_3 data. The cultivars possessing the Pa7 gene are assumed to carry a series of minor genes, covered by Pa7, which govern a LP at least as long as that of 'Vada', a cultivar with a very high level of partial resistance and a long LP.

Introduction

Resistance of barley to leaf rust, *Puccinia hordei* Otth., can be governed by genes conferring a hypersensitive reaction. Roan and Starling (1967) described six such genes, Pa to Pa6. Parlevliet (1976b) concluded that 'Gondar', 'La Estanzuela', 'Cebada Capa' and 'Dabat' all carried the Pa7 resistance gene. This was confirmed by Clifford and Udeogalanya (1976). Another type of resistance reported by Clifford (1972) and Parlevliet (1975, 1976a) and Parlevliet and Van Ommeren (1975) is the paatial resistance, characterized by a reduced rate of epidemic build-up in spite of a susceptible infection type (type 3^+–4). This is caused by the combined action of a a lower infection frequency, a longer latent period, a lower sporulation rate and a shorter infectious period. The latent period is of special importance in partial resistance (Parlevliet and Van Ommeren, 1975; Parlevliet and Kuiper, 1977). This partial resistance is inherited in a polygenic way, since its component, LP, is polygenically controlled (Parlevliet, 1976c).

Van der Plank (1968) assumes that selection for major resistance genes tends to erode the polygenic, partial resistance because the former generally masks the latter. He called this the Vertifolia effect. In the barley-leaf rust system, Pa7 is the only known major gene, which is still effective everywhere in the world (Parlevliet, 1976b). The cultivars carrying this gene were investigated more closely and during this study a high level of partial resistance appeared to be present but concealed by the expression of Pa7.

Materials and methods

'Cebada Capa', 'La Estanzuela' and 'Gondar' were crossed with 'L94', a cultivar not supposed to contribute any genes to partial resistance (Parlevliet, 1975, 1976c; Parlevliet and Kuiper, 1977; Parlevliet and Van Ommeren, 1975). F_2 seedlings were inoculated with leaf rust uredospores and put at 100% r.h. for 16 h. The purpose of this seedling inoculation was to separate the resistant seedlings, carrying the Pa7 gene (infection type 0;), from the susceptible ones not carrying that gene (infection type 4). It is among the latter that possible differences in partial resistance can be expected to show up.

Together with 111 susceptible F_2 plants ten individuals of each parental cultivar and of 'Volla', 'Julia' and 'Vada' were planted out in the greenhouse at a spacing of 0.10 × 0.35 m. They were inoculated in the flag leaf stage and evaluated for LP as described by Parlevliet (1976c).

F_3 plants were studied by growing F_3 lines from a number of selected F_2 individuals. The plants were raised in square plastic pots of 0.12 × 0.12 m, one plant per pot, together with 'L94' and 'Vada' plants. Inoculation and evaluation for LP in the flag leaf stage was done in the same way as in the F_2.

Results

The effect on LP of 10 plants of four cultivars each, and of 111 F_2 plants, not carrying the Pa7 resistance gene for low infection type, is shown in Table 1. The F_2's

Table 1. Latent period for pustule formation in days of four barley cultivars and three F_2 populations, inoculated in the flag leaf stage with leaf rust, *Puccinia hordei*. 'CC' = 'Cebada Capa'; 'Go' = 'Gondar'; 'LE' = 'La Estanzuela'.

Days from inoculation	Number of plants of							
					F_2 of 'L94' with			Σ of
	'L94'	'Volla'	'Julia'	'Vada'	'CC'	'Go'	'LE'	F_2's
9	5							
10	5				1		1	2
11					5	2	2	9
12					9	1	6	16
13					6	2	5	13
14					2	4	7	13
15		3			4	8	10	22
16		6			3	8	4	15
17		1			4		2	6
18			1		1	3	1	5
19			2			1		1
20			5	1		3		3
21			2	2			3	3
22				3	1			1
23				3				
24				1		2		2

Tabel 1. Latentieperiode in dagen van vier gerstrassen en drie F_2 populaties geïnoculeerd in het vlagbladstadium met dwergroest, Puccinia hordei.

Table 2. Latent period for pustule formation in days of eight F_2 plants, of their resulting F_3's and of the cultivars 'L94' and 'Vada' after inoculation with leaf rust, *Puccinia hordei*.

Latent period F_2 plants (days)	Latent period F_3 (days)		Number of F_3 plants evaluated
	mean	range	
9½ ('L94')	13.0	12½–13½	10
10	13.8	12½–15	12
10½	14.3	13 –16	12
11	13.9	13 –16½	12
11	15.4	14 –18	11
14½	14.6	13½–16½	12
18½	21.0	16½–27	11
21	22.8	19½–30	12
23	21.4	17½–24½	11
22 ('Vada')	24.2	22½–26½	10

Tabel 2. Latentieperiode in dagen van acht F_2 planten, van hun F_3's en van de rassen 'L94' en 'Vada' na inoculatie met dwergroest, Puccinia hordei.

ranged from a LP nearly, but not quite, as short as that of the susceptible parent, 'L94', to a LP approximately as long as that of 'Vada', a cultivar assumed to carry some 5 to 6 minor genes for a longer LP (Parlevliet, 1976c). The three F_2's did not differ essentially from one another. The summed F_2 frequencies form a continuous, slightly skewed distribution. A number of F_3 lines, mainly derived from F_2 plants with either short or long LP's was studied and in Table 2 the results from eight representative F_3 lines are shown. The F_2 and F_3 tests were not done simultaneously. The temperatures, not fully controlled, were somewhat lower during the F_3 test than during the F_2 test resulting in longer LP's in the former. Differences in temperature, however, have no effect on the ranking order of the genotypes (Parlevliet, 1975). Out of twenty F_3 lines not a single one was – according to its range – as homogeneous as 'L94' and 'Vada', (F_3 lines with a short LP should be compared with 'L94', those with a long one with 'Vada' (Parlevliet, 1975)). In one F_3 line one plant was observed with a LP as short as that of 'L94'. This was substantiated by comparing F^4 plants derived from this F_3 plant with 'L94' plants for LP. Similarly some of the F_3 lines contained plants with a LP equal to or possibly even surpassing 'Vada' in length of LP. This can be concluded from the fact that the F_3 plants from at least one F_3 line transgressed beyond the range 'Vada' plants showed.

Discussion

Since the susceptible parent 'L94' does not seem to carry any genes governing an increased LP, the genes for LP segregating in the F_2 and F_3 must derive from the cultivars 'Cebada Capa', 'Gondar' and 'La Estanzuela'. These cultivars are morphologically quite similar, they carry the same Pa7 gene (Parlevliet, 1976b) and also segregate in the same way for genes governing LP. This very strongly suggests, that these cultivars are identical and that they have been given different names in different countries.

The discussion therefore proceeds by assuming these cultivars to be identical and

to be designated as 'Cebada Capa'. When all genes segregating in the F_2 originate from one parent only, 'Cebada Capa', no transgression can occur. The F_2 and F_3 plants with the longest LP therefore are a measure of the genetic constitution of 'Cebada Capa' as far as its effect on LP is concerned. This means that 'Cebada Capa' carries genes governing a LP, which is at least as long as the LP effectuated by 'Vada', a cultivar with a very high level of partial resistance and a long LP. In fact, very few genotypes have been found to equal 'Vada' in these respects (Parlevliet and Van Ommeren, 1975; Parlevliet, 1976a). The data presented here, together with those reported earlier (Parlevliet, 1976c) indicate that the long LP of 'Cebada Capa' is governed by a number of minor genes, the number being very likely more than three as otherwise F_3 lines should have been found as homogeneous as the cultivars 'L94' and 'Vada', indicating homozygous F_2 plants (Parlevliet, 1976c). On the other hand the number cannot be very high, ten or more e.g., since the chance of finding genotypes with a LP as short as the susceptible parent 'L94' then becomes remote. This deduction, though, is based on the assumption that the minor genes involved are genetically not linked to each other nor to the Pa7 gene. When linkage occurs the number of minor genes will be higher than suggested here.

Parlevliet and Van Ommeren (1975) observed that LP and partial resistance were highly correlated. This would mean that 'Cebada Capa' has a high level of partial resistance hidden behind the Pa7 gene for hypersensitive resistance. This is quite contradictory to Van der Plank's Vertifolia effect (Van der Plank, 1968). The only satisfactory explanation for this is, that the partial resistance is not fully hidden behind the effect of the Pa7 gene. The expression of this gene appears complete in the seedling stage, only small necrotic flecks are formed (infection type 0;) (Parlevliet, 1976b). In this stage the genes for LP are hardly expressed (Parlevliet, 1975). Also in the heterozygous condition the resistance governed by the Pa7 gene remains complete (infection type 0;). In the adult plant stage this appears different. The infection type of the homozygous parent is slightly increased, some of the necrotic flecks carry a minute pustule (0;–1). The heterozygous F_1 plants has an even higher infection type (0;–2^+), while the F_2 plants carrying the Pa7 gene show a range of infection types from 0;–1 (like the resistant parent) up to 2^+–3^-, beyond the heterozygous F_1 type (Parlevliet, 1976b). He already suggested that in the adult plant stage this Pa7 gene is incompletely dominant and that its expression is affected by modifying factors. The genes for a longer LP can be these modifying factors; the higher the number of these genes the lower the infection type in the F_2 plants. Parlevliet (1976a), in fact, reported, that even in the absence of a gene for low infection type, an increase in LP went together with a decrease in infection type.

Samenvatting

Resistentie van enkele gerstrassen tegen dwergroest, Puccinia hordei; polygene, partiële resistentie overdekt door monogene overgevoeligheidsresistentie

Drie rassen, 'Cebada Capa', 'Gonda', en 'La Estanzuela', die het overgevoeligheidsgen Pa7 bevatten, werden gekruist met 'L94'. Dit ras is buitengewoon vatbaar en bezit vermoedelijk geen genen voor partiële resistntie. De latentieperiode (LP), de belangrijkste component van partiële resistentie, werd gemeten op 111 F_2 planten,

die geen Pa7-gen bezaten, en op vier rassen, die de spreiding voor LP, voorzover bekend, vertegenwoordigden. Ook werd de LP gemeten aan 20 F_3 lijnen. De verdeling van de F_2 voor LP was continu en reikte van bijna even kort als die van 'L94' tot even lang als die van 'Vada' (Tabel 1). De F_3 gegevens bevestigden dit (Tabel 2). De drie rassen met het Pa7-gen worden verondersteld een serie polygenen, overdekt door dit Pa7-gen, te bevatten, welke een LP geven even lang of zelfs langer dan de LP van 'Vada'. Dit laatste ras heeft een zeer hoog niveau van partiële resistentie en een zeer lange LP.

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