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PARTIAL RESISTANCE OF BARLEY TO LEAF RUST, *PUCCINIA HORDEI*. III. THE INHERITANCE OF THE HOST PLANT EFFECT ON LATENT PERIOD IN FOUR CULTIVARS

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SUMMARY

The latent period (LP) in the barley-leaf rust relationship is an important component of the partial resistance complex. The inheritance of the host plant effect on LP was studied in five crosses between four cultivars. The LP, effectuated by the susceptible cultivars L94 and L92, were 8.0 and 8.6 days resp., those of the resistant cultivars Minerva (Mi) and Vada (Va) 16.9 and 17.1 days resp. The mean F_1 and F_2 values of the crosses L92 × L94 and Mi × Va were intermediate between the parental ones. The variances of the F_2's were slightly larger than those of the parents and the F_1's indicating some segregation. In the crosses between a susceptible and a resistant cultivar the F_1 value was half way between the mid-parent and susceptible parent value. The F_2 mean lay approximately half way between the mid-parent and F_1 value, with a distribution positively skewed and slightly bimodal. There was no transgression, in fact not even the parental values were recovered among nearly 500 F_2 plants. The F_3-lines of the crosses between susceptible and resistant cultivars showed within line variances from as low as the parental values to as high as or higher than those of the F_2. In hte F_3's the parental values could be recovered although no transgression occurred.

L94 is supposed to carry no genes effecting a longer LP. The long LP of Mi and Va, assuming no linkage, is thought to be effectuated by the cumulative action of a recessive gene with a fairly large effect and some four to five minor genes with additive inheritance. One of these minor genes is supposed to be carried by L92, while Mi and Va are thought to differ for one minor gene only. In case linkage exists, the number of minor genes involved could be higher.

INTRODUCTION

In barley several types of resistance to leaf rust, *Puccinia hordei* OTTH., have been found (PARLEVLIET, 1976). Partial resistance (slow rusting), thought to be horizontal or race-non-specific by VAN DER PLANK (1963, 1968, 1975), occurs at various levels in many spring barley cultivars (PARLEVLIET & VAN OMMEREN, 1975). This partial resistance, measured by the proportion of disease-affected leaf area, is highly correlated with the latent period (LP), measured in the young flag leaves (PARLEVLIET & VAN OMMEREN, 1975).

The LP, the period between infection (inoculation) and the formation of new uredospores (new pustules becoming visible), varies greatly with cultivars (PARLEVLIET, 1975). The Ethiopian cultivars L92 and L94, both extremely susceptible in the

field, cause a very short LP, the Dutch cultivars Minerva (Mi) and Vada (Va), quite resistant in the field, a long one.

To investigate the inheritance of the host plant's effect on latent period those cultivars were crossed to study their progenies.

MATERIALS AND METHODS

The following crosses were made; L92 × L94, Mi × L94, Va × L92, Va × L94 and Va × Mi. L92 and L94 are early, Mi and Va late heading, two-rowed, spring barleys. L92 is awnless, L94 has hull-less, black grains. Mi and Va, both developed at the IvP from a cross between 'Gull' (= 'Goudgerst') and a primitive or wild barley, resemble each other.

As only a restricted number of plants can be evaluated at the same time the observations were unavoidably spread over a series of experiments, five in total. The experiments 1, 2 and 3, carried out in 1973, 1974 and 1975 respectively served to investigate the parents, the F_1's and the F_2's. The F_3's from the crosses Mi × L94 and Va × L94, derived from F_2 plants of experiment 1, were studied in 1974 (experiment 4). Experiment 5, which was carried out in 1975, comprised the F_3's of the crosses Va × L94 and Va × L92, which derived from the F_2 plants of experiment 2. The number of F_3-lines studied were 55, 51, 33 and 33, respectively. The F_2 plants producing the F_3-lines, were not chosen at random; those with extreme values for the LP were overrepresented in the sample.

All experiments were carried out in greenhouse in the period March to early June. In experiments 1 and 2 the seedlings, grown in small pots, were planted out at a spacing of 0.20 × 0.25 m and 0.10 × 0.35 m, respectively. In experiment 3 the plants were grown in square plastic pots of 0.12 × 0.12 m. The parental and F_1 plants were planted randomly between the F_2 plants. The F_3-lines were sown in rows 1.0 m long and 0.35 m apart, with one F_3-line per row. Per line 20 seeds (1974) or 15 seeds (1975) were sown. Due to different causes, as differential emergence, retarded growth and extreme late heading, the number of plants that could be evaluated varied from line to line between 10 and 20 in 1974 and from 8 to 14 in 1975. Of each parent and corresponding F_2 two rows were included.

In all experiments the inoculation with leaf rust spores was done in the second half of May, when practically all plants were in the flag leaf stage. The spores were dusted on the leaves by means of a cyclone duster. To obtain a more even distribution, the spores were diluted 30 to 50 times with lycopodium spores. After this dusting the plants were kept at a r.h. of approximately 100% for at least 15 h.

The LP of each plant was evaluated by estimating the day at which 50% of the ultimate number of pustules was barely visible (PARLEVLIET, 1975). By this time nearly all successful infections are visible, either as young brown uredosori or as light specks, in the middle of which the uredosori will develop. This evaluation was done on the middle part of the flag leaves of several tillers on each plant. As the Lp is affected strongly by the age of the leaf (PARLEVLIET, 1975) very young and old flag leaves were left out of consideration.

Table 1. Host plant effects on latent period in the young flag leaves of barley inoculated with leaf rust. *Puccinia hordei*. Weighted means of parent, F_1 and F_2 means of three experiments.

Cultivar	Latent period in days				Cultivar
P_1	P_1	F_1	F_2	P_2	P_2
L94	8.0	8.2	8.3	8.6	L92
L94	8.0	10.5	11.6	16.9	Minerva
L94	8.0	10.3	11.8	17.1	Vada
L92	8.6	10.4	11.7	17.1	Vada
Minerva	16.9	17.0	17.1	17.1	Vada

RESULTS

From Table 1 it can be seen, that the susceptible cultivars L94 and L92 caused a short LP, the difference being very small, especially when compared with the LP effectuated by the resistant cultivars Mi and Va. The LP's of the latter two were long and differed very little or not at all. This is in full agreement with earlier observations (PARLEVLIET, 1975; PARLEVLIET & VAN OMMEREN, 1975). The F_1 and F_2 means both were either intermediate (in L92 × L94 and Mi × Va) or tending toward the susceptible parent (in Mi × L94, Va × L92 and Va × L94). The parents L92 and L94, their F_1 and the F_1's of Va × L94, Va × L92 and Mi × L94 were very homogeneous. even more so than the data in Tables 2, 3 and 4 in some cases suggest. This is caused

Table 2. Host plant effects on latent period in days of some barley cultivars, their F_1's and F_2's, inoculated in the young flag leaf stage with leaf rust, *Puccinia hordei*, experiment 1.

Days from inoculation	Number of plants								
	Parent			F_1			F_2		
	L94	Mi	Va	Mi × L94	Va × L94	Va × Mi	Mi × L94	Va × L94	Va × Mi
7	5								
8	10						3		
9					2		22	20	
10				8	8		13	13	
11				2			9	14	
12							5	3	
13							5	11	
14							3	8	
15							6	7	5
16		3	1			2	7	4	12
17		8	4			2	4		18
18		5	8			4			17
19			3						6
20									4
Mean in days	7.7	16.9	17.8	10.2	9.8	17.2	12.5	12.4	17.3

Table 3. As Table 2, experiment 2.

Days from inoculation	Number of plants								
	parent			F_1			F_2		
	L94	L92	Va	L92 × L94	Va × L94	Va × L92	L92 × L94	Va × L94	Va × L92
8	8	2		3			37		
9	2	7		2	1		51	15	23
10					5	9		32	42
11						1		10	11
12								12	10
13								6	7
14								2	2
15			4						
16			5						
17			1						
Mean in days	8.2	8.8	15.7	8.4	9.8	10.1	8.4	10.5	10.4

Table 4. As Table 2, experiment 3.

Days from inoculation	Number of plants										
	parent				F_1		F_2				
	L94	L92	Mi	Va	Mi × L94	Va × L94	L92 × L94	Mi × L94	Va × L94	Va × L92	Mi × VA
8	12	5					80				
9		8					28				
10								15	10	10	
11					13	13		20	13	13	
12								7	11	6	
13								10	15	12	
14								6	7	4	
15								2	3	2	
16										1	3
17			2	5							14
18			10	7							18
19			2	1							14
20											4
Mean in days	8.0	8.6	18.0	17.7	11.0	11.0	8.3	11.6	12.1	11.9	18.0

by the evaluation of the LP in whole days, necessitating the assignement of plants to classes with a day difference. With a range in variation of about half a day, as in the above mentioned cases, plants will fall under either one day (L94 in Table 4) or to two days (L92 in Table 4) depending on the value of their mean. The range of variation in the F_2 of L92 × L94 was larger, slightly more than a day. This, however, did

not find expression in the data of Table 3 and 4 for the same reason, classification in whole days. The cultivars Mi and Va and their F_1 showed a clearly larger variation than the other parents and F_1's. This is caused at least partly by the variation in LP due to variations in age of the flag leaves, an effect hardly noticeable at short LP's, but having marked effects at long one (PARLEVLIET, 1975). The F_2 of Mi $\times$ Va is slightly but significantly more variable than the parents and the F_1. The means of the variances of the two parents and, if present, the F_1 in experiments I and III were 0.66 and 0.35 respectively, those of the F_2 were 1.69 and 1.08 respectively.

In the three crosses between a susceptible and a resistant cultivar the F_2 showed a great deal of variation, the distribution being positively skewed. The F_2 values ranged from slightly longer than the susceptible parent-values toward somewhat shorter than those of the resistant parents. In most F_2's the distribution was bimodal, showing a marked peak at a value approximately equal to the F_1 value and a second, much smaller peak at a higher value (longer LP).

F_3-lines of three crosses were studied and some representatieve data are given in Table 5. The total range of the F_3 was slightly wider than that of the F_2, ranging from the susceptible parent-value (L92) or nearly so (L94) to those of the resistant

Table 5. Effects on latent period in days of some F_3-lines of the barley crosses Va $\times$ L94 and Va $\times$ L92 (experiment 5), inoculated in the young flag leaf stage with leaf rust, *Puccinia hordei*.

Host population	Latent period		
	mean	range	variance
L94	9.2	9 – 9½	0.03
Vada	15.6	15 –16	0.15
F_2	11.2	10 –14	1.30
F_3–14	10.0	10	0.00
F_3– 2	10.2	9½–11	0.18
F_3–27	11.5	10 –14	1.16
F_3–30	11.8	10½–13	0.60
F_3–11	12.0	11 –14½	1.29
F_3– 7	12.8	10 –15	2.10
F_3–13	14.3	13½–15½	0.40
F_3– 6	> 14.5	13½–>16[1]	–
L92	9.5	9½	0.00
Vada	15.7	15 –16	0.14
F_2	11.2	10 –14	0.92
F_3–60	9.7	9½–10	0.03
F_3–69	10.3	9½–11½	0.38
F_3–45	10.4	10 –11	0.15
F_3–54	10.7	9½–13	0.82
F_3–59	11.6	10½–14	1.44
F_3–49	11.8	11½–12	0.07
F_3–52	13.5	13 –14½	0.22
F_3–58	14.5	13 –15½	0.40

[1] In 3 out of 11 plants the LP could not be evaluated because a large proportion of the visible, slightly chlorotic specks did not develop uredosori.

parents. No transgression was observed, although in F_3-6 (Table 5) three plants were found, which produced uredosori with difficulty: the flecks or halo's, however, developed at about the same time as those of Mi and Va.

The variance within the F_3-lines differed greatly, from hardly any, resembling those of L94 and L92, to beyond the F_2-variances. F_3-lines with variances similar to those of the homozygous parents were clearly less frequent in the crosses involving L94 (5 to 7 in 139 F_3-lines), than in the cross with L92 (4 to 6 in 33 F_3-lines).

DISCUSSION

Since no cultivars or lines have been found yet with a LP as short as or shorter than the one of L94, it is assumed, that L94 carries no genes (pairs of alleles) effectuating a longer LP. The small but consistent difference in LP between L92 and L94, and the slightly more variable F_2 compared with the parents and the F_1, suggest that L92 carries one or a few genes (pairs of alleles) affecting LP.

The resistant cultivars Mi and Va, nearly or wholly the same in LP, seem to differ in one or a few minor genes (pairs of alleles) with additive effects. This is indicated by the increased variance and normal distribution of the F_2. Its variance and range, however, are relatively small in comparison with those of the F_2's between the resistant and susceptible cultivars. This implies, that a large part of the genetic complex controlling the long LP of Mi and Va is apparently identical in the two cultivars, which is not surprising in view of their close relationship.

The crosses between the susceptible and resistant parents suggest polygenic inheritance. Among nearly 500 F_2 plants no parental types were recovered, although it might seem so from the data. This is caused by the classification in whole days. The F_2 plants of the crosses Va $\times$ L94 and Va $\times$ L92 (Table 3), evaluated at 9 days, had all in reality a value between 9 and $9^1/_2$ days, while the L94 and L92 plants classified at 9 days, all fell between $8^1/_2$ and 9 days. Only by assuming five or more independently segregating genes (pairs of alleles) with cumulative effects one can explain the lack of parental values among the 500 F_2 plants (the chance to recover a parental type is 2. $(^1/_4)^n$, where n represents the number of segregating loci).

The F_3 data corroborate the polygenic inheritance. The parental values, except L94, have been recovered now. The large variation in within-line variance and the occurrence of F_3-lines with a variance similar to that of the homozygous parents suggest the action of at most six genes, assuming no linkage (the chance of homozygous F_3-lines is $(^1/_2)^n$, where n is the number of loci involved). With seven or more segregating loci no or only very few homozygous F_3-lines are expected among the 172 tested ones, even in this case where the F_3-lines, derived from F_2 plants with fairly short or long LP's, were over-represented. The higher frequency of apparently homozygous lines among the F_3-lines derived from L92 compared with those where L94 was involved suggest the segregation of one or two genes (pairs of alleles) less in the cross with L92 than in the crosses with L94. The one or two genes (pairs of alleles) giving the slightly longer LP period in L92, as assumed from the L92 $\times$ L94 data, seem to be identical with some of the genes present in Mi and Va.

The positive skewness, observed in the F_2, may be explained by one or more of three reasons (SMITH, 1944; HIORTH, 1963):

1) The genes effectuating a shorter LP show dominance. The F_1 means then are expected to be nearer the L94 and L92 values than the F_2 means, which was observed.
2) The genes show geometrically cumulative effects.
3) The lower value represents a physiological barrier and the gene action cannot be expressed fully at such low values.

In the latter two situations the F_1 and F_2 means are expected to be similar. This makes it unlikely, that the observed skweness can be explained by either one or both of the latter reasons alone.

Dominance therefore seems to be involved. The bimodality of the F_2 distribution suggests the action of one dominant gene with a fairly large effect (explaining some 40 to 50% of the difference between the susceptible and resistant cultivars). The remaining four to five genes could be genes with small, additive effects. That no dominance is involved with these minor genes, is suggested by the Mi × Va cross, where one or a few minor genes were assumed to segregate. In case of dominance the F_1 and F_2 means are expected to be lower than the mid-parent value, in stead of similar to it, while the F_2 distribution should be skew, rather than normal.

In this polygenic system dominance and additive effects appear to occur. Inter-allelic interaction may also occur. If not, the F_2 mean is expected to be half-way the F_1 mean and the mid-parent value (described by the equation $F_2 = {}^1/_4.(\overline{P}_1 + \overline{P}_2) + {}^1/_2.\overline{F}_1$, MATHER & JINKS, 1971). The observed F_2 means of the crosses L94 × Mi and L94 × Va were 11.6 and 11.8 days, respectively; the expected values, in the absence of interaction, are 11.5 and 11.4 days, respectively. For the L92 × Va cross the observed and expected values were 11.7 and 11.6 days, respectively. The observed values tend, very slightly, to be higher than the expected ones. This might indicate that interaction effects operating, although insignificant when compared with the dominance and additive effects. These interactions, if present, do not seem to be of a geometrical effect or due to a physiological barrier, as in those cases the observed values should be slightly smaller than the expected values.

There is some other, indirect evidence, that Mi and Va carry a gene with a fairly large effect on LP. Several cultivars with Mi or Va in their parentage e.g. Pauline, Varunda and Vatonga, appear to have a long LP, although the selection for leaf rust resistance was at most a removal of the most susceptible lines.

Summarizing the above it is assumed, that Mi and Va both carry the same recessive gene with a fairly large effect (dominant for short LP) and some four to five minor genes with additive inheritance. One of these minor genes is supposed to be present in L92, while Mi and Va probably differ for one minor gene only. Interaction effects are either absent or of only minor importance. In case of linkage the number of minor genes involved will be higher.

The LP is only one of the components of partial resistance, the others being infection frequency, uredospore production per sorus per day and infectious period. If the host plant effect on each of these components is controlled by some to several genes, with these gene complexes inheriting at least partly independently of one another, partial resistance will inherit in a typically polygenic fashion. This in fact has been reported in several cases e.g. in the maize-*Puccinia sorghi* relationship (Hooker, 1969), the cultivated potato-*Phytophthora infestans* relationship (BLACK, 1970) and the relationship between two wild diploid *Solanum* species and *Phytoph-*

thora infestans (GRAHAM, 1963). About the number of genes involved very little could be said. LUKE et al. (1975) studied slow rusting in oats to *Puccinia coronata* and observed a quantitative distribution in the F_2, slightly skewed with the longer tail toward the resistant parent. They suggested, that the number of genes involved was restricted. However, here too minor and major genes might act together causing an underestimation of the number of genes involved.

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