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RESISTANCE TO WILT IN CHICKPEA. II. FURTHER EVIDENCE FOR TWO GENES FOR RESISTANCE TO RACE 1*

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SUMMARY

Tests of parents and F_1, F_2 and F_3 generations of crosses of JG-62 (early-wilting) and C-104 (late-wilting) with resistant cultivars provide further evidence that resistance in chickpea (*Cicer arietinum* L.) to Race 1 of *Fusarium oxysporum* f.sp. *ciceris* is controlled by at least two genes, both of which must be present in homozygous recessive form for complete resistance. Singly, one of the genes delays wilting, as in C.104. The second has not yet been isolated but crosses of resistant parents with JG-62 suggest that it operates in similar fashion.

INTRODUCTION

UPADHYAYA et al. (1983) demonstrated the existence of differences in the times of wilting of chickpea cultivars in the presence of Race 1 of *Fusarium oxysporum* and evidence was presented that the late-wilting cultivar, C-104, differed from the early wilting JG-62 in respect of a single gene with early-wilting partially dominant to late-wilting. Considering also previous evidence (KUMAR & HAWARE, 1982), it was suggested that resistance to Race 1 was controlled by the segregation of two genes, both of which must be present in homozygous recessive form for complete resistance and, separately, confer late or reduced wilting. The observations offer an explanation for the occurrence of resistant segregants in populations of crosses where both parents were susceptible.

This report presents further evidence for the segregation of two genes, obtained from tests of the parents and F_1, F_2, and F_3 generations of crosses of JG-62 and C-104 with some of the resistant parents reported in the earlier study (KUMAR & HAWARE, 1982).

MATERIALS AND METHODS

Two tests were conducted in a screenhouse in 37 cm diameter plastic pots, containing a potting medium inoculated with a single spore culture of Race 1 of *Fusarium oxysporum* f.sp. *ciceris* (HAWARE & NENE, 1982).

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Between the two tests JG-62 was sown and the time of wilting recorded for each pot to check the uniformity of inoculum. Pots in which wilting was much delayed were rejected and the data from the second test were adjusted to take account of the time of wilting of JG-62, which varied from 14 to 24 days after sowing. The JG-62 debris was incorporated in the soil to make the inoculum more uniform.

The first test included the parents and F_2 generations of crosses of the four resistant genotypes (BG-212, T-3, P-436-2 and WR-315) with JG-62. There was one pot each of the resistant parents, seven pots of JG-62, twelve of C-104 and six or seven pots each of the F_2 populations. The pots of JG-62 and C-104 formed part of the earlier study reported in Part I (UPADHYAYA et al., 1983).

In the second test, the parents and F_1 and F_2 generations of the crosses of BG-212 and T-3 with C-104, and F_3 progenies of BG-212 × C-104 were compared. Two pots were sown of each of the parents and F_1s and 14 of the F_2 generations. In addition, four pots of JG-62 were sown to assess the time of early wilting.

Twenty to twenty-five seeds were sown in each pot and the pots were completely randomised in both tests. The number of days from sowing to the appearance of initial wilt symptoms was recorded for each plant. The means and variances were calculated for each cultivar and generation and the F_2 and F_3 generations classified as early or late-wilting for chi square tests of goodness of fit to expected ratios.

RESULTS

In neither test did any plants of the resistant parents wilt and they were therefore classified as resistant. In the first study, JG-62 wilted earlier than C-104 and exhibited a much lower variance (Figure 1). Furthermore, their distributions overlapped, a few C-104 plants wilting as early as JG-62. The possible reasons and the consequent problems of accurate classification of early and late wilting genotypes in segregating populations were discussed in part I.

In the F_2 populations, the numbers of resistant plants gave excellent fits to 15:1 ratios (Table 1), providing further evidence for the segregation of two genes, with resistant individuals homozygous recessive at both loci. Moreover, there were clear discontinuities in the numbers of days to initial symptoms, occurring about 18 days after sowing and coinciding with the point of overlap of JG-62 and C-104. The separation of early- and late-wilting plants at this point gave good fits to the expected 9:6:1 ratios of early and late-wilting and resistant plants in three of the four crosses and overall.

In the second test, JG-62 again wilted earlier than C-104 and showed a smaller spread (Figure 2). Although the distributions overlapped, it was to a smaller extent than in the first study.

The F_1s wilted nearer to the time of C-104 indicating dominance of late wilting over resistance. In the F_2s the numbers of late wilting and resistant plants were consistent with the segregation of a single gene (χ^2 3:1 = 0.79 and 0.08; P = 0.30–0.50 and 0.70–0.80) with late wilting dominant. The majority of the susceptible plants wilted later than JG-62, although there was some extension beyond the ranges of C-104 and the F_1s, especially in the cross of T-3 and C-104.

Of the 60 F_3 progenies of the cross of BG-212 and C-104, 30 segregated resistant

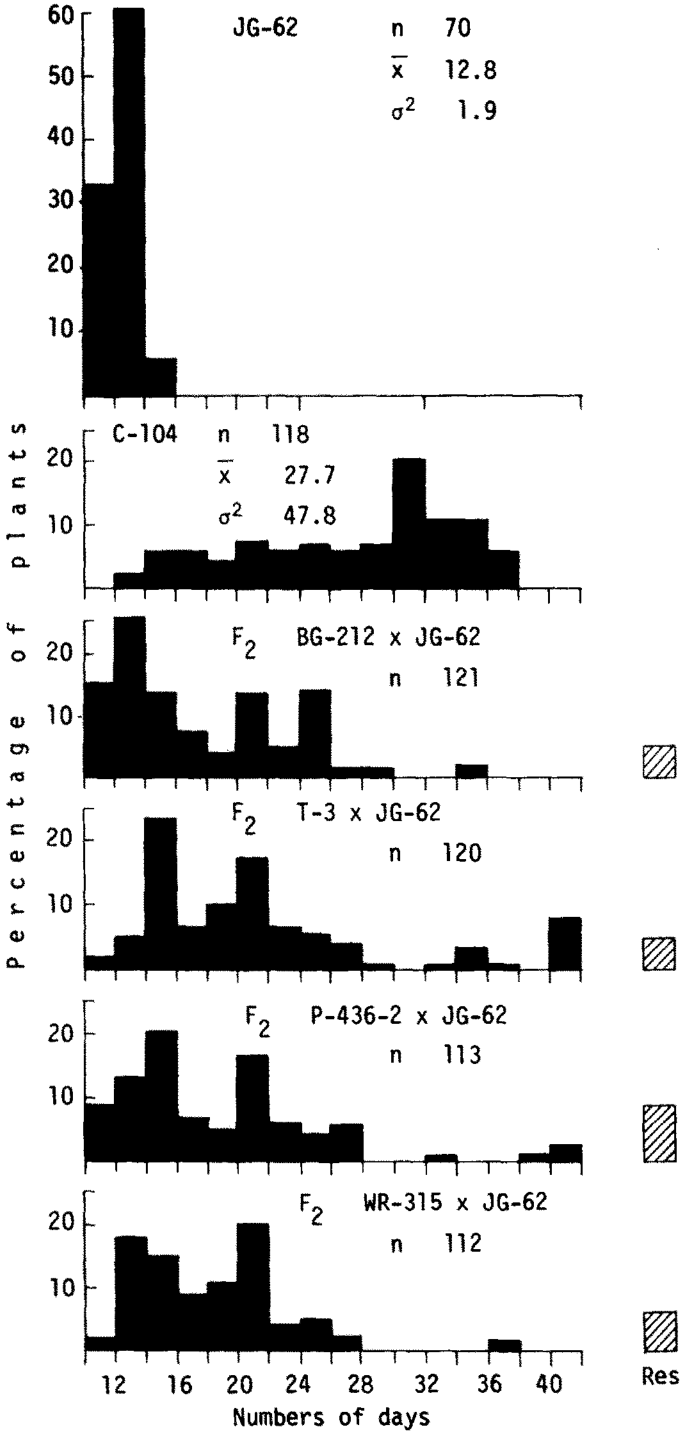

Fig. 1. Percentage frequencies for numbers of days from sowing to appearance of initial wilt symptoms in chickpea cultivars JG-62 and C-104 and four F_2 populations of crosses involving JG-62 after exposure to *Fusarium oxysporum* f.sp. *ciceris* (first test).

Table 1. The numbers of early and late-wilting and resistant chickpea plants after exposure to *Fusarium oxysporum* f.sp. *ciceris*, chi squared values and probabilities for goodness of fit to the expected ratios in F_2s of crosses of JG-62 and four resistant parents.

Cross	Numbers of plants			15 susceptible*: 1 resistant		9 early : 6 late: 1 resistant	
	early wilting	late wilting	resis-tant	χ^2	P	χ^2	P
BG-212 × JG-62	79	36	6	0.34	0.50–0.70	4.06	0.10 –0.20
P-436-2 × JG-62	60	43	10	1.30	0.20–0.30	1.38	0.50 –0.70
WR-315 × JG-62	57	47	8	0.15	0.50–0.70	1.30	0.50 –0.70
T-3 × JG-62	51	63	6	0.32	0.50–0.70	11.53	0.001–0.01
Total	247	189	30	0.03	0.80–0.90	2.05	0.30 –0.50
Heterogeneity				2.08	0.50–0.70	16.23	0.01 –0.02

* Early and late-wilting plants.

and late-wilting plants, 14 were uniformly late wilting, and 16 were uniformly resistant, which fitted well with the ratio of 1 late-wilting : 2 segregating : 1 resistant, expected from the segregation of a single gene ($\chi^2 = 0.13$, P = 0.90–0.95). Further, the numbers of late-wilting and susceptible plants in the segregating progenies fitted well to 3:1 ratios (Table 2).

DISCUSSION

The data presented here and in earlier reports (KUMAR & HAWARE, 1982) provide evidence that the inheritance of resistance in chickpea to Race 1 of *Fusarium oxysporum* is controlled by at least two genes.

The cultivar C-104 appears to differ from WR-315 and CPS-1 in respect of a single locus with susceptibility dominant to resistance (KUMAR & HAWARE, 1982). C-104 was demonstrated to differ from JG-62 in respect of a second locus, which results in delayed wilting when in homozygous recessive form (UPADHYAYA et al., 1983).

The current data are consistent with these observations. The problems of accurate classification of early and late-wilting plants, especially where parental distributions overlap and where F_2 distributions do not show complete discontinuity, were discussed by UPADHYAYA et al. (1983). Clearly, segregation ratios may be distorted by the inclusion of individuals in the wrong categories, but the distortion can be expected to be small since misclassification would occur in both directions. This is supported by the good fit to 9:6:1 ratios obtained in three of the F_2 populations of crosses of resistant parents with JG-62. In the F_2 of T-3 × JG-62 the fit was not good but the margin between early and late wilting is small and easily obscured by environmental effects and in this case movement of the point of separation by only two days gives a good fit to the expected ratios.

Furthermore, the numbers of susceptible (early- and late-wilting) and resistant plants, which are not prone to misclassification, fit very well indeed to the expected ratios of 15 susceptible : 1 resistant in all cases.

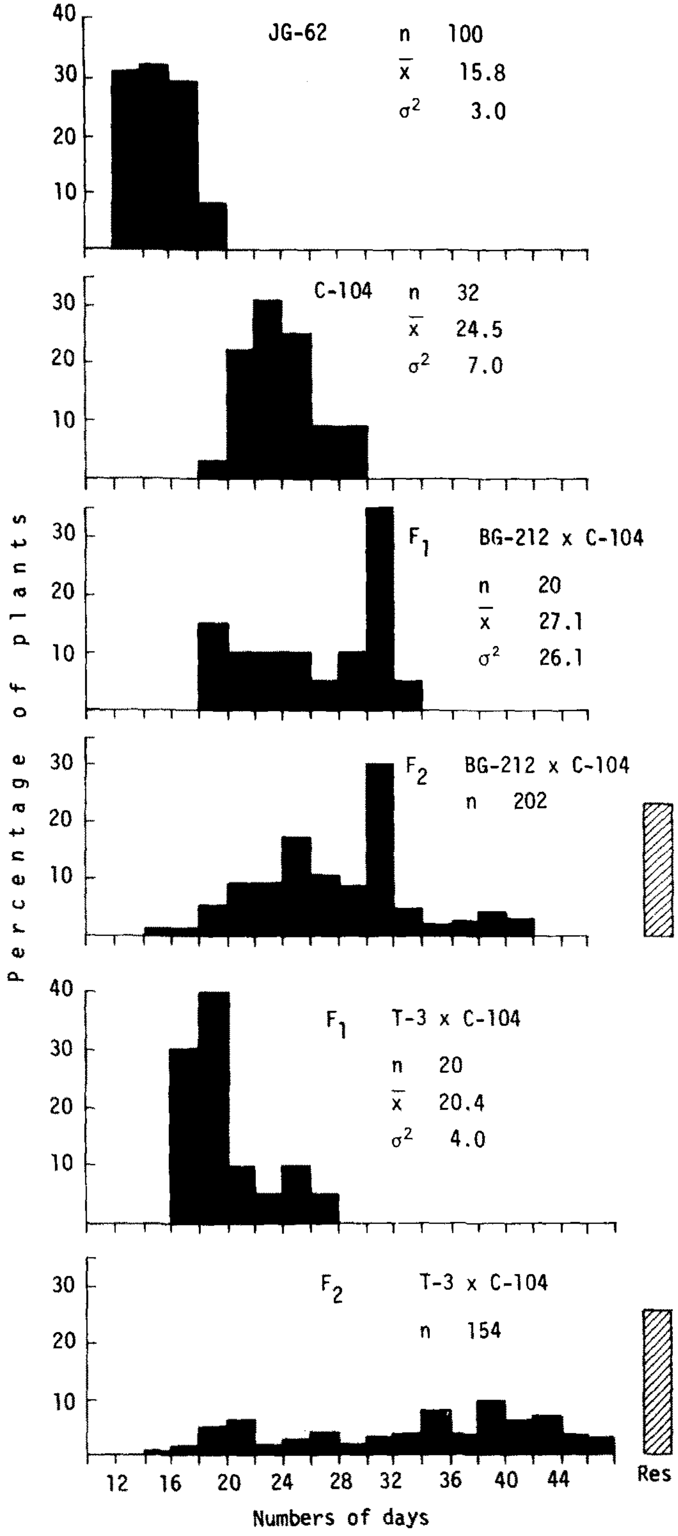

Fig. 2. Percentage frequencies for numbers of days from sowing to appearance of initial wilt symptoms in chickpea cultivars JG-62 and C-104 and F_1 and F_2 populations of crosses involving C-104 after exposure to *Fusarium oxysporum* f.sp. *ciceris* (second test).

Table 2. The numbers of susceptible and resistant chickpea plants in segregating F_3 progenies of the cross BG-212 × C-104 afer exposure to *Fusarium oxysporum* f.sp. *ciceris* and chi squared values and probabilities of goodness of fit to 3:1 ratios.

Progeny No.	Number of plants		χ^2	P
	susceptible	resistant		
4	28	12	0.53	0.30–0.50
5	29	6	1.15	0.20–0.30
7	46	14	0.09	0.70–0.80
8	19	4	0.71	0.30–0.50
10	26	12	0.88	0.30–0.50
16	32	8	0.53	0.30–0.50
23	25	10	0.24	0.50–0.70
24	8	4	0.44	0.50–0.70
26	5	2	0.05	0.80–0.90
31	25	8	0.01	0.90–0.95
32	8	6	2.38	0.10–0.20
33	27	10	0.08	0.70–0.80
37	30	8	0.32	0.50–0.70
38	7	2	0.04	0.80–0.90
48	26	14	2.13	0.10–0.20
51	17	4	0.40	0.50–0.70
53	30	13	0.63	0.30–0.50
57	24	11	0.77	0.30–0.50
58	19	5	0.22	0.50–0.70
60	23	9	0.17	0.50–0.70
62	23	5	0.76	0.30–0.50
63	24	11	0.77	0.30–0.50
65	16	6	0.06	0.80–0.90
66	24	12	1.33	0.20–0.30
67	7	3	0.13	0.70–0.80
68	17	9	1.28	0.20–0.30
70	18	8	0.46	0.30–0.50
72	17	5	0.06	0.80–0.90
74	37	13	0.03	0.80–0.90
75	11	4	0.02	0.80–0.90
Total	648	238	1.64	0.20–0.30
Heterogeneity			15.03	0.98–0.99

Accepting the above reservations, the data are consistent with the hypothesis that JG-62 carries the two genes in homozygous dominant condition ($H_1H_1H_2H_2$); C-104 is homozygous recessive at the second locus ($H_1H_1h_2h_2$); and the resistant parents are homozygous recessive at both ($h_1h_1h_2h_2$). The resistant allele at the first locus has not yet been isolated but the time of wilting among susceptible plants in F_2 populations of crosses of JG-62 and resistant parents suggest that it also delays wilting, although the extent of the delay has not yet been determined. Many other late-wilting genotypes have been identified. For example, K-850 has been shown to wilt about the same time as C-104 while H-208 is intermediate. One of these may be homozygous recessive at the first locus.

Susceptible plants were rare or absent in crosses among the resistant parents used in the present study and another resistant cultivar, CPS-1, (KUMAR & HAWARE, personal communication) indicating their resistance to be under similar genetic control. The occurrence of susceptible plants in crosses of two resistant parents may indicate the involvement of other, perhaps polygenic complexes, and this would also explain the extended times of wilting recorded in the present study in some populations, particularly in the F_2 of T-3 × C-104. This suggestion will require further study.

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