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Inheritance of Resistance to *Fusarium solani* f.sp. *Phaseoli* in Beans (*Phaseolus vulgaris* L.) and Breeding Strategy to Transfer Resistance[1]

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Abstract. **Susceptibility to root rot in beans** *Phaseolus vulgaris* **incited by** *Fusarium solani* **(Mart.) Appel & Wr. f.sp.** *phaseoli* **(Burk.) Snyd. & Hans. was dominant in crosses between resistant PI 203958 and susceptible cultivars 'Cascade', 'Falcon', 'State Half Runner' and 'California Small White'. A quantitative inheritance pattern for disease reaction was observed. Selection of F_2 plants showing slight disease symptoms resulted in F_4 populations with a lower disease index than the unselected F_2 population, indicating substantial gain. The results suggested that breeding methods such as recurrent selection, which are more suitable for improving quantitative traits than are backcrossing or pedigree selection, should be used to develop,** *Fusarium* **root rot resistant bean populations and cultivars.**

Fusarium root rot of beans is a significant problem in bean growing areas throughout the world. Since modification of cultural practices is not a wholly effective means of control, the development of root rot resistant cultivars is necessary. The first resistant dry bean cultivars were released in 1974[3], but no resistant snap bean cultivars are available.

Conflicting interpretations of the inheritance of root rot resistance in beans have been reported. McRostie (5) studied the cross of 'Flat Marrow' with 'Robust Pea Bean' in field and greenhouse tests and concluded that two duplicate recessive genes were involved. Yerkes and Freytag (10) obtained root rot resistant F_1 plants from a *Phaseolus vulgaris* × *P. coccineus* cross, which suggested that resistance from *P. coccineus* was dominant over susceptibility. Azzam (1) used PI 165435 and *P. coccineus,* line no. 2014 as resistant parents in crosses with OSC 22. Results of field and greenhouse tests indicated three recessive genes governed resistance in PI 165435, but the F_2 ratios did not show good agreement to a classical Mendelian ratio. Progenies from *P. coccineus* reacted similarly, with 2 or 3 major recessive genes being involved. Smith and Houston (7) used 7 resistant parents, including N203 (PI 203958), in crosses with 10 susceptible cultivars. All artificially inoculated F_1 parents were susceptible and few resistant plants were found in three F_2 families. In the other 4 families, 16-19% of the plants were found to be resistant, suggesting a 13:3 ratio and that resistance was controlled by 1 dominant and 1 recessive gene. The F_3 families resulting from 'Sutter Pink' × N203, 'California Red' × N203, and 'California Red' × PI 165435 also gave 14-18% resistant plants which agreed with the hypothesis. Smith later reported (6) that no true breeding lines had been obtained, which would indicate that the inheritance was more complex than previously thought. Their results involving PI 165435 differed from those obtained by Azzam, but different susceptible parents were used and another *Fusarium* isolate may have been employed.

Wallace and Wilkinson (8) found root rot resistance to have complex inheritance. From field studies, Bravo et al. (3) concluded that resistance to *Fusarium* in N203 and *P. coccineus* resulted from 3 or more primarily dominant genes and that additive gene effects were greater than dominance effects. Hassan et al. (4) published more detailed results in which N203 was estimated to possess about 4, and strain 2114-12 about 6 primarily dominant genes for resistance. The narrow sense heritabilities were .26 and .44 in progenies from the 2 parents, respectively. However, when the inoculum concn was doubled, the means of the F_1 and F_2 generations shifted towards susceptibility. In greenhouse tests using young plants, gene action was essentially additive, but in the field experiments where older plants were scored for root rot reaction, gene action was shifted to partial dominance. It is evident from these reports that the testing procedures as well as sources of resistance and plant age influence the results of inheritance studies.

Since knowledge of the inheritance is critical to designing optimum breeding strategies for incorporating a particular trait into economically-useful populations, we studied crosses of resistant N203 (PI 203958) with several susceptible cultivars to obtain additional information about the inheritance of resistance to root rot incited by *Fusarium solani* f.sp. *phaseoli* and to determine the improvement in resistance from an initial cycle of recurrent selection.

Materials and Methods

Parents were grown and crosses made in the greenhouse. The following populations were studied using the nutrient culture technique described by Boomstra et al. (2). The F_1, F_2, BCP_1, BCP_2, and F_4 progenies derived from selected F_2 plants of 'Cascade' × PI 203958 (hereafter designated CN); F_1, F_2, and F_4 progenies from selected F_2 plants of 'Falcon' × PI 203958 (FN); F_3, and F_4 and F_5 progenies from selected F_3 and F_4 plants, respectively of 'California Small White' × PI 203958 (WN); and F_2 and F_3 progenies from selected F_2 plants of 'State Half Runner' × PI 203958 (SN). Plants from each population were inoculated and placed at random in the tanks, and seedlings of the susceptible and resistant parents were included as checks. Results from different tanks were compared and later pooled when they were found to be homogenous. F_1 and backcross progeny from the CN cross and F_2 progenies from the FN cross were studied using a greenhouse pot test (2) to compare disease reactions of plants subjected to different conditions. Pots were placed at random on a greenhouse bench, with susceptible and resistant parents included as checks.

Seedlings were rated as having slight, moderate or severe symptoms based on the intensity of hypocotyl (lesions) and

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Table 1. Distributions of plants in different root rot reaction classes (*Fusarium solani* f.sp. *phaseoli*) within progenies derived from crosses of 'Cascade' × PI 203958 and 'Falcon' × PI 203958. The nutrient culture technique was used.

Pedigree and generation	No. of plants	Distribution Infection type slight	 moderate	 severe	Disease index^z
Cascade (P_1)	150	0	0	150	100.0
PI 203958 (P_2)	150	100	50	0	30.0
F_1 ($P_1 \times P_2$)	26	0	12	14	76.9
F_2	338	9	29	300	93.6
F_4^y	376	125	158	93	52.4
BCP_1	14	1	2	11	87.1
BCP_2	109	2	31	76	84.3
Falcon (P_3)	120	0	0	120	100.0
PI 203958 (P_2)	120	80	40	0	30.0
F_1 ($P_3 \times P_2$)	5	0	1	4	90.0
F_2	546	15	39	492	94.6
F_4^y	282	113	120	49	46.7

^{z}Slight - 20, moderate = 50, severe = 100.

^{y}Total of several F_4 families, derived from selected F_2 plants.

vigor of the foliage, with values of 20, 50 and 100, respectively being assigned. The disease index of each family was computed as the mean value of individual plant ratings.

F_2 plants that were resistant based on results of the nutrient culture technique were selected and transplanted into pots filled with soil. Only a few F_3 seeds were obtained, so F_3 plants were grown without further selection to produce F_4 seeds. Progeny testing was used to verify the accuracy of selection since discrete segregation ratios were not obtained in the F_2. To evaluate the effectiveness of selection, disease indices of the unselected F_2 generation and F_4 families derived from F_2 plants showing only slight symptoms were compared.

Results and Discussion

F_1, F_2, and backcross data indicated that susceptibility was dominant over resistance in the CN and FN families evaluated using the nutrient culture technique (Table 1). These populations did not show discrete segregation patterns, but rather a complex inheritance. The disease indices of the F_1 generations were closer to the susceptible rather than the resistant parent, and few resistant plants were recovered in the F_2 and backcross families. When assuming that 1) two recessive genes are primarily responsible for resistance, and 2) the moderately infected plants are, in fact susceptible, there were too many susceptible plants in the F_2 and backcross families to fit this hypothesis. The deficiency of resistant segregates may be due to some misclassifications, or minor genes could be involved in resistance. The following factors may also contribute to the lack of discrete segregation ratios. Classification of infection types was somewhat arbitrary, and different ratios would have been realized if different classification criteria had been used. Moderate infection types may not constitute a definite class or the low resistance of some plants might not have been stable.

Table 2. Distributions of plants in different root rot reaction classes (*Fusarium solani* f.sp. *phaseoli*) within progenies derived from crosses of 'State Half Runner' × PI 203958 and 'California Small White' × PI 203958. The nutrient culture technique was used.

Pedigree and generation	No. tested	Distribution slight	 Infection type moderate	 severe	Disease index^z
State Half Runner × PI 203958					
F_2	102	4	12	86	91.0
F_3y	25	16	8	1	32.8
California Small White × PI 203958					
F_3	264	9	10	245	95.4
F_4^x	23	7	10	6	53.9
F_5^w	40	37	3	0	22.3

^{z}Slight = 20, moderate = 50, severe = 100.

^{y}Derived from selected F_2 plants.

^{x}Derived from selected F_3 plants.

^{w}Derived from selected F_4 plants.

Table 3. Distributions of plants in different root rot reaction classes (*Fusarium solani* f.sp. *phaseoli*) within progenies derived from crosses of 'Cascade' × PI 203958 and 'Falcon' × PI 203958. The greenhouse pot test was used.

Pedigree and generation	No. tested	Distribution slight	 moderate	 severe	Disease index^z
Cascade (P_1)	50	0	2	48	98.0
PI 203958 (P_2)	50	33	17	0	30.0
F_1 ($P_1 \times P_2$)	15	10	5	0	30.0
BCP_2	80	33	31	16	47.6
Falcon (P_3)	30	0	2	28	97.0
PI 203958 (P_2)	30	20	10	0	30.0
F_2 ($P_3 \times P_2$)	342	14	63	265	87.5

^{z}Slight = 20, moderate = 50, severe = 100.

The F_4 families were derived through the F_3, from F_2 plants selected as being resistant. All F_4 families continued to segregate, and none was either completely susceptible or resistant, suggesting that minor genes may be involved. The average disease indices of the F_4 families were considerably lower than those of the F_2 populations from which the resistant selections were derived. Selection in the F_2 generation produced improved F_4 populations but continued selection is necessary to establish uniform resistant lines. The populations derived from the crosses of N203 with 'California Small White' and 'State Half Runner' followed similar segregation patterns, and gain from selection in the tested progenies from selected F_2 or F_3 plants was similar (Table 2).

The F_1 and backcross data from the CN cross obtained using the greenhouse pot test (Table 3), did not agree with results obtained using the seedling tank test (Table 2), but were similar to the results of Hassan et al. (5), who also used N203 as a resistant parent and a similar pot testing procedure. They found resistance to be dominant over susceptibility. The F_2 populations from the FN cross reacted similarly to the populations analyzed using the seedling tank test, but results differed from those of Hassan et al. (4).

These studies provide no additional conclusive evidence concerning the mode of inheritance of *Fusarium* resistance. We found, as did Hassan et al. (4), that the inheritance patterns were influenced by the testing procedures employed, age of plants, and the parents involved. The improved level of resistance of F_4 families derived from F_2 plants showing a slight reaction suggested that resistance was heritable. The disease indices of the F_2 populations varied from 93.2 to 96.1, while those of the F_4 populations derived from the CN and FN crosses were 52.4 and 46.7, respectively. The disease index (35.3) of one F_4 family from the CN cross approached the index of N203 (30.0), and several others were below 45.

Pedigree selection and backcross breeding have been used extensively to transfer disease resistance into desirable strains. However, complex inheritance and low heritability have limited

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the success of attempts to incorporate *Fusarium* resistance into bean cultivars, although sources of resistance have been known for more than 50 years (9). Wallace and Wilkinson (8) found root rot resistance from N203 and 2114-12 to be quantitatively inherited. They suggested the desirability of intercrossing superior individuals which could be backcrossed later to appropriate recurrent parents for developing acceptable cultivars. Bravo et al. (3) found sizable additive gene effects although resistance was largely dominant over susceptibility. They emphasized the need for progeny tests to determine resistant lines. Hassan et al. (4) suggested that highly resistant, homozygous selections could be differentiated from partially resistant, heterozygous ones only by progeny testing.

Recurrent selection was developed as a systematic method to increase the frequency of favorable genes or gene combinations while retaining the genetic variability within a breeding population. It has not been used widely in breeding self-pollinated crops because of the extensive crossing required and the time and effort involved. Several studies have indicated the need for intercrossing and cyclic selection programs (4, 9) based on apparent quantitative inheritance of resistance and linkage to undesirable traits. Our results from an initial cycle of selection support the feasibility of this approach.

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Glucose Metabolism in Petals of Senescing Roses[1]

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Abstract. **The pentose phosphate shunt (PPS) was shown to be active in roses (*Rosa hybrida* L.). The C_6/C_1 ratio indicated that possibly as much as 50% of the glucose oxidized in the rose flower is through the PPS. However, the activity of the PPS in relation to the Embden-Meyerhof-Parnas pathyway-tricarboxylic acid cycle (EMP-TCA) pathway did not change significantly throughout the cut life of the rose. There was a drop in the respiratory rate of petals throughout the cut flower life. The inner petals exhibited a consistantly higher respiratory rate than did outer petals regardless of whether the flower was kept in water or preservative.**

In many higher organisms glucose may be respired through two major oxidative pathways – the TCA cycle and the PPS. The relative activity of the pathways may change during the growth and development of the plant or plant organs. In corn root tips, the PPS became more active as the roots became older (1). Also, immature tissue of several plants respired glucose almost exclusively by way of the TCA; the PPS became more active as the tissue aged, eventually accounting for 50% of the respired CO_2 (10). Beets in an active growing phase showed little PPS activity, but the activity increased with aging in dormant tissue (13). In tissue culture, the activity of the PPS decreased as the growth rate increased (18).

Diseased plants are known to go through a process similar to aging. When infected, plants produce phenolic compounds which prevent further spread of the disease but which also destroy tissue around the lesion (8). Quinones and caffeic acid (9) or their derivatives are thought to be responsible for necrosis and death of diseased tissue. The phenolic compounds are synthesized from products arising from the PPS. Possibly, as tissue senesces, the PPS becomes more active, phenols are produced in greater quantities and the organ eventually senesces.

The purpose of this investigation was to determine if the relative activity of the TCA and PPS changed during senescence, and to determine if a preservative had an effect on the activity of the two pathways.

Materials and Methods

'Forever Yours' roses were harvested when the sepals were parallel to the stem and brought to the laboratory where the stems were recut to 30.5 cm in length and all leaves were removed. The flowers were graded according to stem diameter, flower head size and degree of opening, and placed in uniform replications. The flowers were then put into bottles containing either distilled water or a preservative consisting of 8-hydroxyquinoline citrate (8-HQC) (0.24 g/liter) and sucrose (22.44 g/liter). The flowers remained at about 24°C with continuous fluorescent light of 19 lux for the duration of the experiment.

The relative activity of the TCA and PPS was estimated by the C_6/C_1 ratio which is determined by measuring the respired

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