

Oligogenic Inheritance of Length of Latent Period in Six Slow Leaf-Rusting Wheat Cultivars

Tae Soo Lee and Gregory Shaner

Former graduate student and professor, respectively, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907.

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ABSTRACT

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The inheritance of latent period of *Puccinia recondita* on wheat was studied in crosses of slow- and fast-rusting cultivars inoculated with *P. recondita* in the greenhouse. Analyses of F₃ families and F₁ backcrosses for Morocco/SW 72469-6 and L574-1/Suwon 92 showed that the long latent period in slow-rusting wheats SW 72469-6 and L574-1 was conditioned by

two partially recessive genes with equal effects. Latent period and uredinium size were negatively correlated. The long latent period in CI 10745 and Milyang 8-6 were conditioned by two recessive genes with equal effect. The long latent period was controlled by one or two recessive genes in P65113B6, and by three recessive genes in P6028A2.

Additional key words: durable resistance, genetics, *Triticum aestivum*.

The wheat leaf rust fungus, *Puccinia recondita* Rob. ex Desm., was one of the earliest pathogens of wheat to be recognized (4). For the last 30 yr, leaf rust has been the most important rust disease in soft red winter wheat. The use of cultivars that carry genes for hypersensitive resistance has been one of the most effective and economical means of controlling rusts on cereals. But the short-lived nature of hypersensitive resistance has led to a search for alternative forms of resistance (16,34).

Slow-leaf-rusting resistance, which appears to be race-nonspecific and durable, has been found in wheat and efforts to find cultivars with this resistance have continued for the last several years. Slow leaf-rusting wheat cultivars infected with *P. recondita* exhibit longer latent periods, smaller and fewer uredinia, and less spore production than susceptible cultivars. In the field, the effects of these slow-rusting components are cumulative over several infection cycles, resulting in slow leaf rust development (24). Latent period is one of the most important components of slow-rusting resistance (8,11,17,18,25). Several wheat cultivars with slow leaf-rusting resistance have been identified (3,10,17,22,23,25).

The objectives of this study were to determine the genetic control of the long latent period in several slow-rusting cultivars of diverse origin.

MATERIALS AND METHODS

Experiments in the greenhouse were carried out with 10 different populations derived from crosses between slow-rusting wheat cultivars and two fast-rusting cultivars. These 10 populations were basically composed of one combination of crosses: slow-rusting cultivar/fast-rusting cultivar.

Fast-rusting cultivars Morocco and Suwon 92, and slow-rusting cultivars P6028A2-9-5-6-1 (P6028), Suwon 85, L574-1, and CI 10745 have been the subject of earlier reports (10,11,17,22,23,25). The slow-rusting cultivars Milyang 8-6 and SW 72469-6, both from South Korea, and slow-rusting Purdue breeding line P65113B6 were also included.

Seedlings in the one-leaf stage were vernalized at 3 C for 8-10 wk and then were transplanted individually into 500-ml plastic pots containing standard greenhouse soil mix. Plants were grown in a greenhouse and natural daylight was supplemented by

incandescent and fluorescent light providing about 167 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ for 16 hr each day from transplanting to maturity.

When a plant reached the preboot to early-heading stage, the adaxial surface of the flag leaf was inoculated with urediniospores of culture 7434-1-1T of *P. recondita*. This culture is virulent to all wheat cultivars used in this experiment and was described previously (10). A DeVilbiss atomizer operated at about 0.35 $\text{kg} \cdot \text{cm}^{-2}$ of air pressure was used to apply 1.2 mg of freshly collected urediniospores in 0.6 ml of distilled water per plant. That quantity of inoculum was sufficient to give more than 70% disease severity (as rated according to Cobb's [19] modified scale) on susceptible plants. After inoculation, the plants were sprayed lightly with distilled water, kept in a moisture chamber for 14-16 hr, and then returned to the greenhouse bench. All experiments were conducted in the greenhouse in the late fall and early spring and will be referred to as fall and spring greenhouse cycles, respectively. The mean greenhouse temperature was 23 C.

The latent period was calculated by first estimating the proportion of visible infection sites that had developed into uredinia on each flag leaf each day from 6 days after inoculation until all the infection sites (flecks) had erupted into uredinia. By regression of the probit of the proportion of uredinia erupted on the number of days following inoculation, T_{50} (the day by which 50% of the uredinia had erupted) was calculated as an estimate of the latent period of each plant (21).

On each plant, the lengths and widths of 10 uredinia per flag leaf were measured with an ocular micrometer at 21 and 25 days following inoculation. The size of a uredinium was calculated as:

$$\text{Size} = (\text{length} \times \text{width} \times \pi) / 4.$$

Level of dominance was calculated as the deviation of the mean latent period of the F₁ from the latent period of the midparental value divided by one-half of the difference between parental latent period means (1). The modified parent-offspring regression method (11,29) was used to estimate the heritability of latent period for the L 574-1/Suwon 92 and SW 72469-6/Morocco crosses. This formula is:

$$H = [(100 \bar{X} b_{yx}) / \bar{Y}] / 2/3$$

in which \bar{X} is the mean of the F₂ generation from which the F₃ families were derived, \bar{Y} is the unweighted mean of the F₃ family means, and b_{yx} is the slope of the regression of y on x (15). The fraction 2/3 is used to correct the upward-biased heritability in b_{yx} caused by inbreeding in the F₂ population (29). Based upon latent

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period data for parents and F_1 and F_2 populations, a genotypic hypothesis was constructed which was tested by comparing the observed and expected latent periods and patterns of segregation shown by F_3 families and the backcross populations.

The chi-square (χ^2) goodness-of-fit test was used for analyzing data from the F_2 populations (30).

RESULTS

Morocco/SW 72469-6. The latent periods of both parents, the F_1 and F_2 , and F_3 family means are summarized in Fig. 1. The F_2 plants were grown during the 1980 fall and 1982 spring greenhouse cycles; F_1 plants, F_3 families, and the parental populations were grown during the 1981 spring greenhouse cycle. The parents and F_1 plants were tested again in the 1982 spring greenhouse cycle along with both backcross F_1 populations (Fig. 2). Even though mean latent periods of F_1 and parents from the 1981 and 1982 spring greenhouse cycles were not significantly different, latent period data from the two greenhouse cycles were not combined because a 0.5-day longer latent period was observed in SW 72469-6 during the spring 1981 greenhouse cycle. Only the latent period data of the F_1 and parents from the 1981 spring greenhouse cycle were used for constructing expected latent periods for each different genotype of F_3 families. The data from the spring 1982 cycle were used for both backcross populations.

In the 1981 and 1982 spring greenhouse cycles, latent period of SW 72469-6 ranged from 8.6 to 12.3 days as opposed to the significantly shorter period of 5.6 to 6.7 days for Morocco. The mean latent period of the F_1 was midway between the short latent period parent and midparental value. Degree of dominance was 0.59 for the short latent period. The frequency distributions of latent period of F_2 plants and F_3 family means were continuous, unimodal, and skewed toward the shorter latent period. Since no transgressive segregation was observed in F_2 plants and F_3 families,

it was concluded that the short latent period parent, Morocco, did not possess any genes to contribute to longer latent period in this cross.

One- and three-gene models were ruled out because frequencies of each parental type observed among F_3 families were too low to fit the one-gene model and too high to fit the three-gene model. In the one-gene model there should have been 17.5 families of each parental type; in the three-gene model there should have been 1.1 families of each parental type. Of 73 families, there were four each of the short and long latent period parental types, which better fit the two-gene model. The 1981 spring greenhouse cycle involved 73 families with 8–17 plants per family, of which 70 families had 10–17 plants per family. Under the two-gene model, F_3 families derived from the $AaBb$ genotype would be segregating for two genes (where A and B designate loci controlling latent period and a and b are the alleles for longer latent period). To obtain a 90% probability of having at least one plant of each genotype, 35.6 plants are needed, and for 95% probability, 46.3 plants are needed. Since no F_3 families had more than 17 plants, it was very difficult to identify families derived from doubly heterozygous F_2 plants with any certainty. F_2 genotypes other than $AaBb$ would segregate for only one gene or be nonsegregating. For F_3 families that segregate for only one gene, 10.4 and 8.1 plants are needed to have 95% and 90% probabilities of getting at least one plant of each genotype, respectively. Seventy F_3 families were classified into one of the F_2 genotypes based upon F_3 family mean, evidence of segregation within the family, and range of latent periods. The χ^2 analysis (Table 1) showed that the data fit a two-gene model very well ($0.5 < P < 0.75$).

The latent period of the backcross to SW 72469-6 was significantly longer than the latent period of the F_1 or backcross to Morocco (Fig. 2). The F_1 mean latent period in the 1982 spring greenhouse cycle showed a 0.65 degree of dominance for short

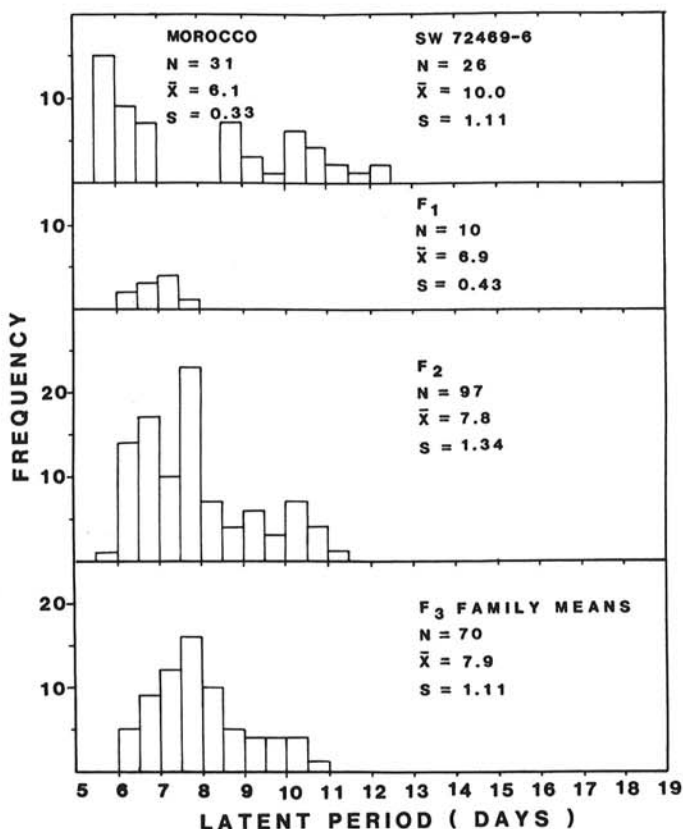


Fig. 1. Frequency distributions of latent periods of leaf rust on wheat cultivars Morocco, SW 72469-6, and the F_1 , F_2 , and F_3 family means of the cross between Morocco and SW 72469-6. (N = number of plants or families, \bar{X} = population mean (days), and S = population standard deviation).

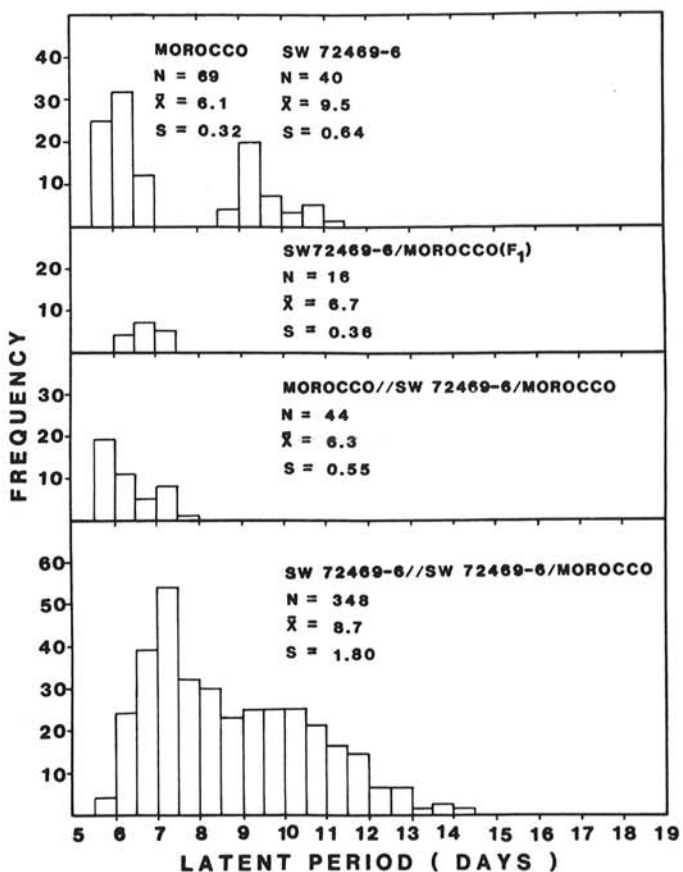


Fig. 2. Frequency distributions of latent periods of leaf rust on wheat cultivars Morocco, SW 72469-6, and F_1 and both backcross F_1 populations of the cross between Morocco and SW 72469-6. (N = number of plants, \bar{X} = population mean (days), and S = population standard deviation).

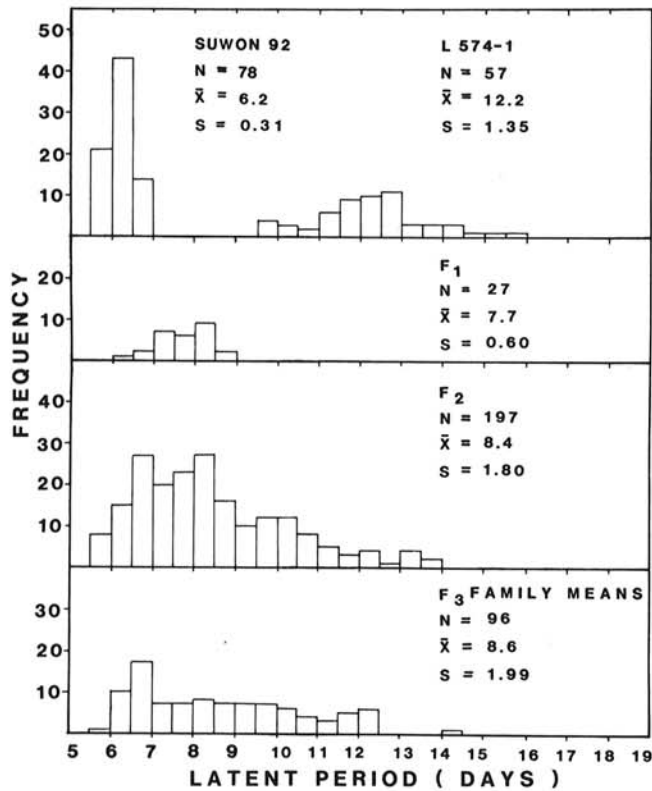


Fig. 3. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 92, L574-1, and the F₁, F₂, and F₃ family means of the cross between Suwon 92 and L574-1. (*N* = number of plants or families, \bar{X} = population mean (days), and *S* = population standard deviation).

latent period compared with a 0.59 degree of dominance in the 1981 spring greenhouse cycle. The backcross means and distribution also seemed to fit the predicted two-gene model with an equal degree of dominance (0.65) for shorter latent period. Using the 70 families with 10–17 plants per family, heritability for latent period was estimated to be 46%.

The correlation coefficient of latent period and uredinium size in F₂ plants was -0.71 .

L574-1. F₂ plants from the cross L574-1/Suwon 92 were grown during the 1980 and 1981 fall greenhouse cycles. F₁ plants, F₃ families, and the parental population were grown during the 1981 fall greenhouse cycle. The backcross populations L574-1//L574-1/Suwon 92 and Morocco//L574-1/Morocco were tested in the greenhouse (1982 spring) along with parent cultivars and the F₁ of L574-1/Morocco. Since the mean latent periods of the F₂ plants were not significantly different in the 1980 and 1981 fall greenhouse cycles, the F₂ data from both greenhouse tests were combined. The latent periods of the two parents (L574-1 and Suwon 92), the F₁, F₂, and F₃ family means are summarized in Fig. 3. The latent periods on L574-1 plants ranged from 9.6 to 15.5 days and those on Suwon 92 ranged from 5.8 to 6.7 days. The range for latent period on F₁ plants overlapped with the latent period range of the susceptible parent, Suwon 92, but not of the slow-rusting parent, L574-1. Based on the mean latent period of F₁, the shorter latent period of Suwon 92 was partially dominant with a 0.5 degree of dominance. The distribution of latent periods of F₂ plants was continuous, skewed toward shorter latent periods, and bimodal. The frequency distribution of F₃ family mean latent periods was similar to that of F₂ populations: continuous and skewed towards a shorter latent period without transgressive segregation. The expected frequencies of each parental family under one-, two-, and three-gene models were 24, 6, and 1.5, respectively. Since nine F₃ families behaved like the short latent period parent and seven families behaved like the slow-rusting parent, some information was provided concerning

TABLE 1. Expected and observed F₃ family segregation for latent period of infection by *Puccinia recondita* in the wheat cross Morocco/SW 72469-6, assuming two genes of equal effect

Genotype	F ₃ plants		F ₂ genotype					Total	<i>P</i>
	Predicted latent period (days)		<i>AABB</i>	<i>AaBB</i> or <i>AABb</i>	<i>AaBb</i>	<i>AAbb</i> or <i>aaBB</i>	<i>Aabb</i> or <i>aaBb</i>		
Expected segregation within F ₃ family									
<i>AABB</i>	6.1	1	1	1					
<i>AaBB</i> or <i>AABb</i>	6.5		2	4					
<i>AaBb</i>	6.9			4					
<i>AAbb</i> or <i>aaBB</i>	8.05		1	2	1	1			
<i>aaBb</i> or <i>Aabb</i>	8.45			4		2			
<i>aabb</i>	10.0			1		1	1		
Expected F ₃ family mean latent period									
		6.1	6.8	7.5	8.05	8.7	10.00		
Expected ratio of F ₃ families									
		1	4	4	2	4	1		
F ₃ families with 10–17 observations									
No. observed		4	14	24	7	17	4	70	
No. expected		4.375	17.5	17.5	8.75	17.5	4.375	70	
Contribution to χ^2		0.032	0.7	2.414	0.35	0.014	0.032	3.542	0.750 > <i>P</i> > 0.500
Range of observed F ₃ family mean latent period									
		6.1–6.2	6.3–7.2	7.2–7.9	8.0–8.3	8.3–10.2	9.8–10.7		

genetics of long latent period in L574-1. The data for the 96 F_3 families supported the two-gene hypothesis with a probability level of $0.50 < P < 0.75$ (Table 2). Under the two-gene model, 17 plants per family are sufficient to distinguish nonsegregating families from those segregating for one gene, but are not sufficient to detect segregation for two genes with high probability.

The latent periods of L574-1, Suwon 92, Morocco, and their F_1 and backcross F_1 populations are summarized in Fig. 4. Since the mean latent period of the F_1 of L574-1/Suwon 92 was longer than that of the F_1 of L574-1/Morocco by 0.3 day, a predicted latent period for each different genotype in L574-1//L574-1/Suwon 92 populations was calculated from the F_1 of L574-1/Suwon 92 and its parents, and the expected latent period of each genotype in Morocco//L574-1/Morocco was calculated from the F_1 of L574-1/Morocco and its parents.

The mean latent period of the F_1 backcross to L574-1 was significantly longer than the latent period of the L574-1/Suwon 92 F_1 and of the F_1 of the backcross to Morocco. The L574-1/Suwon 92 mean latent period showed a 0.5 degree of dominance for shorter latent period compared with the F_1 of the L574-1/Morocco which showed a 0.6 degree of dominance. The χ^2 goodness-of-fit test of backcross populations fit the two-gene model. The value of the χ^2 test was 7.67 with a probability level of 0.1–0.25. Estimated heritability for latent period was 61%.

The correlation coefficient of latent period and uredinium size on F_2 plants grown in 1980 was -0.55 .

CI 10745/Morocco. Latent period ranges of CI 10745, Morocco, and F_1 of CI 10745/Morocco were from 8 to 10.8 days, 5.5 to 6.7 days, and 6.7 to 7.8 days, respectively (Fig. 5). The frequency distribution of latent period for F_2 plants was continuous and

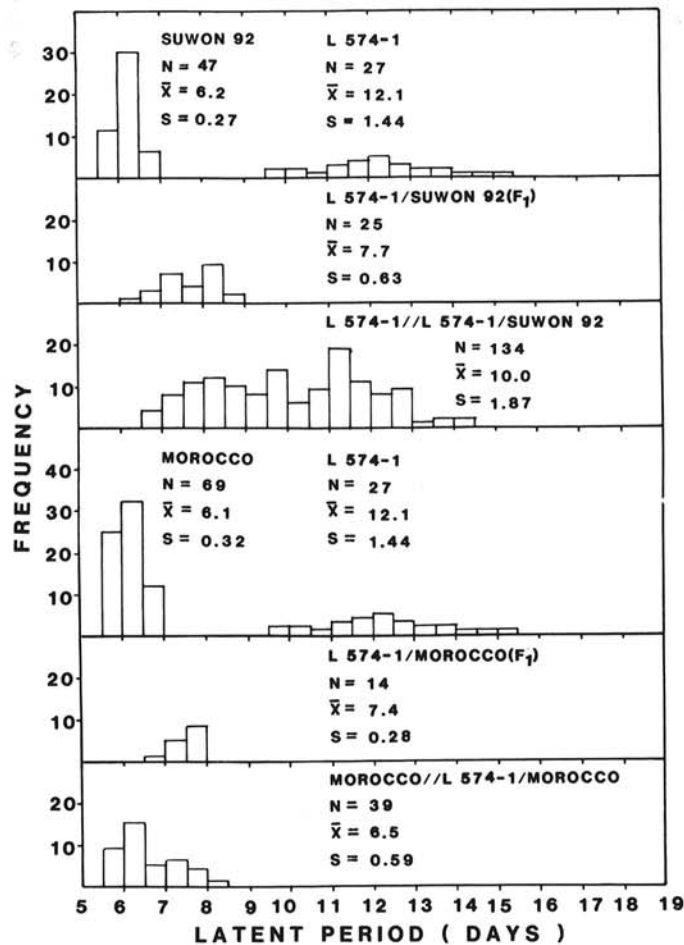


Fig. 4. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 92, L574-1, Morocco, and F_1 and backcross F_1 populations of the crosses L574-1/Morocco and L574-1/Suwon 92. (N = number of plants, \bar{X} = population mean (days), and S = population standard deviation).

skewed towards a shorter latent period. There was no transgressive segregation and the degree of dominance was 0.38 for a shorter latent period. Of 182 F_2 plants, 19 plants had latent periods within the range of CI 10745, 39 plants had a latent period shorter than the mean of the short latent period parent, Morocco. The χ^2 test for the F_2 population better fit the two-gene model than the one- and three-gene models. The value of the χ^2 for the two-gene model was 5.41 with a probability level of 0.1–0.25. Values of χ^2 were too high to fit the one- and three-gene models. Thus, the hypothesis that two recessive genes condition long latent period was considered most probable.

The mean latent period of the F_1 backcross to CI 10745 was longer than that of the F_1 backcross to Morocco (Fig. 5). Of the 27 plants from the CI 10745//CI 10745/Morocco cross, 10 plants had latent periods within the range of CI 10745 and 17 plants fell within the range of F_1 of CI 10745/Morocco. Of the 45 plants from the Morocco//CI 10745/Morocco cross, 20 plants had a shorter latent period than the mean latent period of Morocco and 25 plants fell within the range of the F_1 plants. The data from these backcross

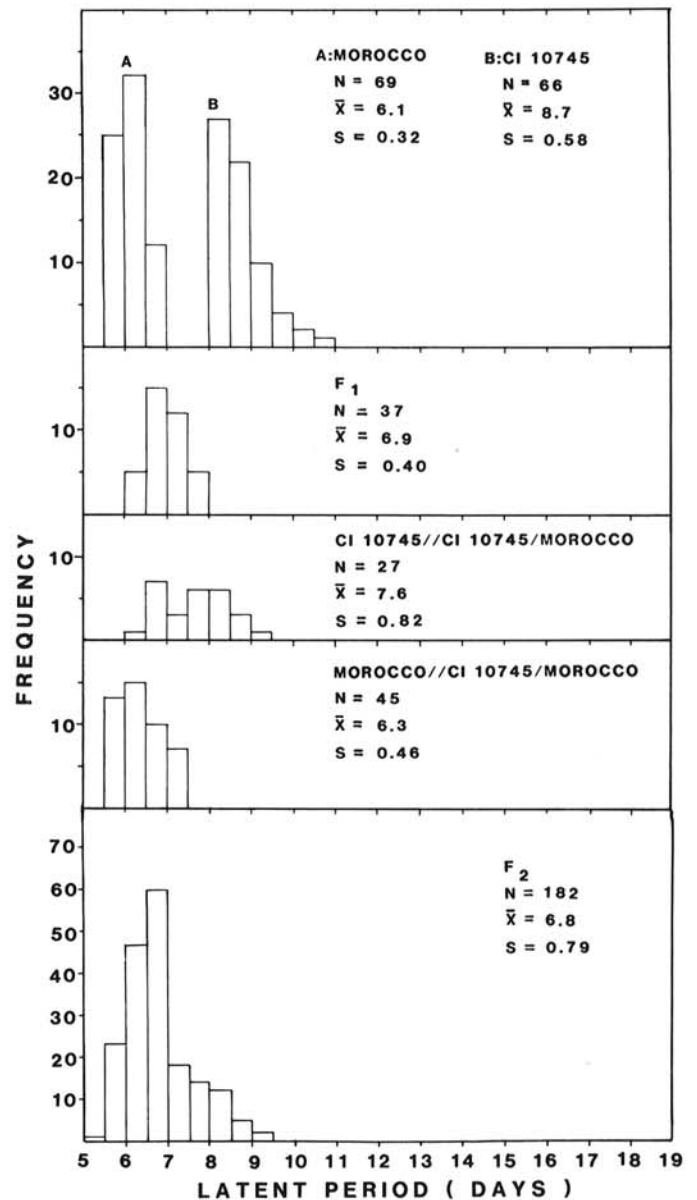


Fig. 5. Frequency distributions of latent periods of leaf rust on wheat cultivars Morocco, CI 10745, and the F_1 , F_2 , and both backcross F_1 populations of the cross between Morocco and CI 10745. (N = number of plants, \bar{X} = population mean (days), and S = population standard deviation).

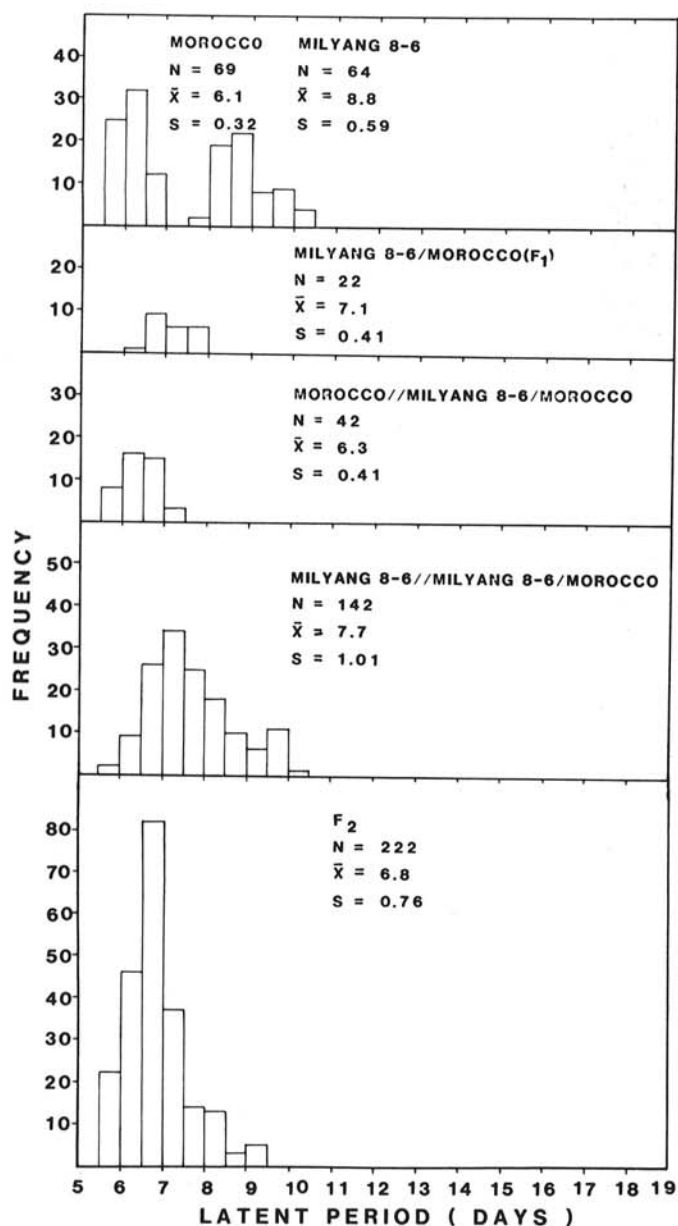


Fig. 6. Frequency distributions of latent periods of leaf rust on wheat cultivars Morocco, Milyang 8-6, and the F₁, F₂, and both backcross F₁ populations of the cross between Morocco and Milyang 8-6. (N = number of plants, \bar{x} = population mean (days), and S = population standard deviation).

populations supported with equal probability either a one-gene or two-gene model and thus would support the hypothesis that long latent period in CI 10745 is conditioned by one or two recessive genes.

CI 10745/Suwon 92. The F₂ population was almost normally distributed. The mean latent period of F₁ plants (7.4 days) was almost midway (7.45 days) between the two parents, indicating incomplete dominance for short or long latent period. Of 139 F₂ plants, 30 segregated for the latent period of the resistant parent CI 10745, 33 for the susceptible parent Suwon 92, and 76 for F₁ plants. But, of the 76 F₂ plants segregating for the latent period of the F₁, eight were distributed through the range of Suwon 92 and four were distributed through the range of CI 10745. Even without adjusting the overlapping plants for each category, the results gave a good fit to the 1:2:1 ratio expected for an incompletely dominant monogenic mode of inheritance. The value of χ^2 on the F₂ plants was 1.35 with a probability level of 0.50–0.75. Because data from F₂ plants of CI 10745/Morocco did not fit the model of monogenic inheritance and mean latent periods of the F₁ and F₂ plants of CI 10745/Suwon 92 were longer than those of F₁s and F₂ plants from CI 10745/Morocco (by 0.5 and 0.6 day, respectively), monogenic control of long latent period in CI 10745 was questioned. Since the latent period of Suwon 92 is longer than that of Morocco by 0.1 day, the relatively longer latent periods in the CI 10745/Suwon 92 cross might result from modifying factors possessed by Suwon 92 or CI 10745. The modifying factors might lengthen the latent period of the CI 10745/Suwon 92 cross without transgressive segregation. Similar differences were observed from the F₁ of L574-1/Suwon 92 and L574-1/Morocco (Fig. 4).

Milyang 8-6/Morocco. Latent periods of Milyang 8-6 ranged from 8 to 10.3 days compared to a range of 5.5 to 6.7 days for Morocco (Fig. 6). The mean latent period of Milyang 8-6 was significantly longer than that of Morocco. The frequency distribution of latent period for F₂ plants was continuous and skewed toward a shorter latent period with 0.26 degree of dominance for shorter latent period. There was no transgressive segregation. Of 222 F₂ plants, 21 plants fell within the range of Milyang 8-6 while the other 201 plants fell within the range either of Morocco or the F₁. It was very difficult to classify these 201 F₂ plants according to genotypes because the range of latent period distributions for Morocco and the F₁ plants overlapped. Out of 222 F₂ plants, 55.5 resistant parental types are needed to fit the one-gene model and 13.9 plants are required by the two-gene model. Considering the number of F₂ plants of the Milyang 8-6 latent period phenotype, it appears that the long latent period in Milyang 8-6 is conditioned by two recessive genes.

The mean latent period of the backcross Milyang 8-6//Milyang 8-6/Morocco was significantly longer than the mean latent period of the backcross Morocco//Milyang 8-6/Morocco (Fig. 6). The frequency distribution of 142 progeny of the backcross to Milyang 8-6 was continuous and almost normally distributed. The observed mean latent period and distribution of the Milyang 8-6//Milyang

TABLE 2. Expected and observed F₃ family segregation for latent period of infection by *Puccinia recondita* in the wheat cross L574-1/Suwon 92, assuming two genes of equal effect

F ₃ family	AABB	AABb or AaBB	AaBb	AAbb or aaBB	Aabb or aaBb	Total	P
Expected F ₃ family mean latent period	6.2	7.3	8.5	9.2	10.3	12.2	
Expected No. of F ₃ families	6	24	24	12	24	6	96
Observed no. of F ₃ families	9	26	23	9	22	7	96
Contribution to χ^2	1.5	0.167	0.042	0.75	0.167	0.167	2.793
Range of observed F ₃ family mean latent period	5.9–6.2	6.3–7.4	7.5–9.3	8.6–9.9	9.6–12.0	11.9–14.4	0.75 > P > 0.50

^aExpected family mean latent periods are based on two gene model with equal effect and 0.5 degree of dominance. The expected numbers of families are also based upon Table 1.

8-6/Morocco population fit the expected two-gene model well. For the two-gene hypothesis, at least 35.5 parental types are needed, and for the three-gene hypothesis 17.75 plants are needed. Because 46 plants had latent periods within the range of Milyang 8-6, it is concluded that long latent period in Milyang 8-6 is conditioned by two recessive genes with equal effects. The observed mean latent period and distribution of the F₁ backcross to Morocco also appear to agree with the two-gene model.

P6028A2/Morocco. As expected, mean latent period of P6028A2 (11.4 days) was significantly longer than that of Morocco (6.1 days) (Fig. 7). Latent periods of P6028A2 ranged from 10.5 to 12.7 days and those of Morocco ranged from 5.5 to 6.7 days. The mean latent period of F₁ plants was 6.5 days and ranged from 6.1 to 7.5 days. The distribution of latent periods of the F₂ population was continuous and skewed toward shorter latent period. There was no transgressive segregation. Because of the high degree of dominance (0.73) for shorter latent period, latent period distributions of Morocco and the F₁ plants overlapped from 6.1 to 6.7 days. Of the 185 F₂ plants, four plants had latent periods in the range of P6028A2, and 126 plants had latent periods in the range of either F₁ plants or Morocco. The remaining 54 plants segregated for latent periods between 7.6 and 10.4 days, an interval between the F₁ and P6028A2. Out of 185 F₂ plants, 2.9 plants of each parental genotype are expected with a three-recessive-gene model and 11.6 plants are expected for a two-recessive-gene model. Thus, the four resistant parental types observed in the F₂ population better fit the three-recessive-gene model than the two-recessive-gene model.

Suwon 92/P65113B6. The frequency distributions of latent periods of Suwon 92, P65113B6, and the F₁ and F₂ populations of the Suwon 92/P65113B6 are summarized in Fig. 8. The mean latent period of P65113B6 (8.6 days) was significantly longer than that of Suwon 92 (6.5 days). Latent periods of P65113B6 ranged from 7.9 to 10.3 days and those of Suwon 92 from 5.5 to 6.7 days. The latent periods of F₁ plants ranged from 6.6 to 7.8 days with a mean of 7.2 days. The latent periods of the F₂ population were almost normally

distributed with a mean latent period of 7.6 days. The F₂ displayed transgressive segregation for long latent period. Of 160 F₂ plants, 54 plants had latent periods within the range of P65113B6, 79 plants had latent periods within the range of the F₁, 17 plants had latent periods within the range of Suwon 92, and the remaining 10 plants segregated for both F₁ plants and Suwon 92 (the range of latent periods of F₁ plants and Suwon 92 varied from 6.6 to 6.7 days). Of 160 F₂ plants, 40 and 10 plants of each parental type are needed to fit the one- or two-gene hypothesis, respectively. The 54 observed P65113B6 parental types in the F₂ population indicated that long latent period of P65113B6 might be conditioned by one recessive gene with 0.17 degree of dominance towards shorter latent period.

DISCUSSION

The latent period distributions of F₂ populations of most crosses between slow-rusting wheat cultivars and fast-rusting wheat cultivars were continuous and skewed toward the shorter latent period. The lack of discrete classes of latent period in the F₂ might occur if latent period is not conditioned by mono- or oligogenes. However, continuous distributions in F₂ populations do not necessarily indicate polygenic inheritance (31). A normal distribution of a phenotypic trait can be seen from the segregation of only one gene in F₂ populations when heritability is less than 50%. Hoff and McDonald (7) studied the resistance of pine (*Pinus monticola*) to *Cronartium ribicola*. The distribution of the number of infections per linear millimeter of needle from the progenies of crosses between resistant and susceptible pines was continuous and almost normal. Even though estimated heritabilities were as low as 34% in one group and 40% in another group, they found that their data fit well the assumption of a single, incompletely dominant gene. Kuhn et al (11) reported that F₃ family mean latent periods of

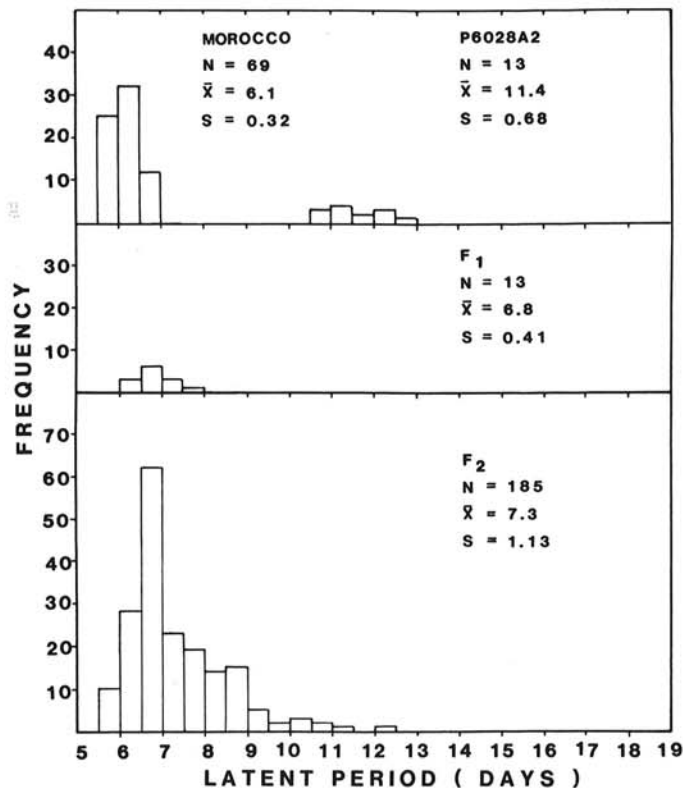


Fig. 7. Frequency distributions of latent periods of leaf rust on wheat cultivars Morocco, P6028A2, and the F₁ and F₂ populations of the cross between Morocco and P6028A2. (N = number of plants, \bar{X} = population mean (days), and S = population standard deviation).

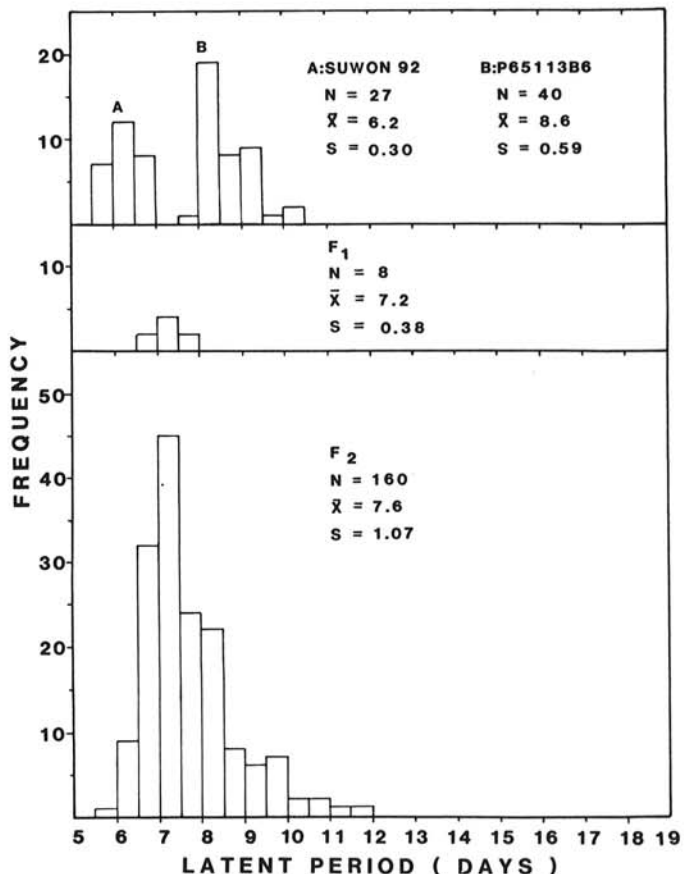


Fig. 8. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 92, P65113B6, and the F₁ and F₂ populations of the cross between Suwon 92 and P65113B6. (N = number of plants, \bar{X} = population mean (days), and S = population standard deviation).

a cross between slow leaf-rusting wheat Suwon 85 and fast rusting wheat Suwon 92 were continuously distributed, but classification of the F₃ families provided evidence that long latent period of Suwon 85 is conditioned by two recessive genes. Heritability for latent period, estimated by regressing F₃ on F₂ and correcting for inbreeding, was 46%. They concluded that the large environmental variation in relation to genetic variation made it difficult to determine the number of loci involved based on observations of a single plant.

The observed distributions of F₃ mean latent periods of Morocco/SW 72469-6 and L574-1/Suwon 92 in this study also did not reveal distinct classes. However, distributions of both backcross F₁ populations and segregation within F₃ families provided evidence that long latent periods in SW 72469-6 and L574-1 are conditioned by two recessive genes in each case. Distributions of latent periods of backcross F₁ populations of CI 10745/Morocco and Milyang 8-6/Morocco were also consistent with the hypothesis that two recessive genes condition long latent period. It is difficult to determine the number of genes conditioning long latent period in crosses between a slow-rusting and a fast-rusting wheat without either F₃ populations or backcross populations. Even though more than 25% of F₂ plants of the Morocco/SW 72469-6 cross segregated for SW 72469-6 latent period phenotype and about 30% of F₂ plants from the L574-1/Suwon 92 cross (Fig. 3) segregated for L574-1 latent period phenotype, the evidence indicates that the long latent periods of the two slow-rusting cultivars are conditioned by two recessive genes. Thus, about 34% of slow leaf-rusting parental types recovered from F₂ plants of Suwon 92/P65113B6 do not necessarily indicate that long latent period of P65113B6 is controlled by a single gene. It is possible that the long latent period of P65113B6 may be conditioned by one or two recessive genes, and that that of P6028A2 is conditioned by three recessive genes.

Several published reports on the inheritance of slow-rusting in small grains indicate that it is conditioned by one to 21 genes (6,9,13,20,28). Since all of these studies were done in the field, high environmental variances might have increased the estimated number of genes. These studies measured slow-rusting as disease development in the field and may have included the effects of several components of resistance.

The rationale for stability of polygenic general resistance is based in part upon genetic probabilities. To overcome polygenic resistance completely, races of a pathogen must accumulate all the necessary virulence genes to overcome the effect of the host resistance genes. Since the acquisition of each virulence gene by a pathogen is presumably an independent event, the pathogen may need a long period of time to overcome polygenic resistance of the host (26,32). Moreover, selection pressure on the pathogen is not nearly as great with partial resistance as with hypersensitive resistance (32). Some researchers have insisted that general resistance is not always polygenic resistance nor is polygenic resistance always general (durable) resistance. Eenink (5) considered that the stability of resistance is dependent upon the genetics of host-pathogen interactions and not upon the genetics of resistance. Therefore, it is not correct to predict that polygenic resistance is stable and mono- or oligogenic resistance is unstable. In Indiana, Caldwell (2) observed the gradual, but complete, loss of polygenic adult-plant hypersensitive resistance in a relatively short period of time against *P. recondita* in a wheat cultivar derived from Chinese Spring. Vanderplank (33) reported that Selkirk wheat with five genes for vertical resistance had been severely infected by *P. graminis* f. sp. *tritici* in the southern part of North America. Luke et al (13,14) reported that slow-rusting resistance protected Red Rustproof oats against *P. coronata* for more than 30 yr by lessening yield loss and disease severity.

The estimated heritabilities for latent period in crosses Morocco/SW 72469-6 and L574-1/Suwon 92 were 46 and 61%, respectively. Heritability estimates for slow-rusting resistance in small grains have ranged from 23 to 92% (6,8,9,13,27,28,35).

In our study, mean latent periods and distributions of latent periods of susceptible wheat cultivars Morocco and Suwon 92 were almost the same (6.1 days for Morocco and 6.2 days for Suwon 92).

The F₂ populations of crosses between Morocco and any slow-rusting wheat cultivar have not shown any transgressive segregation, but the distributions of F₂ populations of crosses between Suwon 92 and certain slow-rusting wheat cultivars such as Suwon 92/P65113B6, and Suwon 92/Suwon 85, did show transgressive segregation. Even though the distribution of latent periods of F₂ populations of CI 10745/Suwon 92 showed no transgressive segregation, the mean latent period of the F₂ population was 0.6 days longer than that of CI 10745/Morocco. All of these results indicate that Suwon 92 may have modifier genes that contribute to a longer latent period in crosses with certain other slow leaf-rusting wheat cultivars, such as P65113B6 and CI 10745.

Since the mean latent periods of F₁ and F₂ populations of CI 10745/Suwon 92 were longer than that of CI 10745/Morocco, it is expected that the level of slow-rusting in F₁ populations may depend upon the fast-rusting parent in each cross.

Based on experiments in the greenhouse, Kuhn et al (11) reported that latent period was negatively correlated with uredinium size. They suggested that long latent period and small uredinium size were possibly controlled by genes in common. Our results also showed a moderately high negative correlation coefficient between latent period and size of uredinia in F₂ populations of Morocco/SW 72469-6 (-0.71) and L574-1/Suwon 92 (-0.55). The moderately high correlation between latent period and uredinium size indicates that both of these traits might be controlled by some genes in common. Selection for long latent period of *P. recondita* on wheat should not be difficult and would tend to select for small uredinia as well.

Potential problems inherent in incorporation of resistance from unadapted cultivars into a breeding program are the possible introduction of unknown susceptibility to a nontarget pathogen or linkage between the genes controlling disease resistance and agronomically undesirable traits such as late maturity, height, and weak straw (1). Fortunately, the long latent periods of slow-rusting wheat cultivars CI 10745, L574-1, P6028A2, P65113B6, SW 72469-6, and Suwon 85 appear to be associated with neither agronomically undesirable traits nor with susceptibility to other diseases (23).

Good progress can be expected in a breeding program for slow-rusting resistance by making crosses between high yielding, good quality soft wheat lines and these slow leaf-rusting lines. The resistance of wheats with different genes for slow leaf-rusting should be more durable than monogenically inherited hypersensitive resistance (12).

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