

Resistance

**Transgressive Segregation of Length of Latent Period in Crosses Between Slow Leaf-Rusting Wheat Cultivars**

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**ABSTRACT**

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Six slow-rusting wheat cultivars were intercrossed to determine whether each cultivar possessed unique genes for long latent period during infection by *Puccinia recondita*. All crosses showed transgressive segregation. Within some transgressively segregating F<sub>2</sub> populations, some plants had latent periods shorter than either parent and as short as that of the fast-rusting cultivar Morocco. Other F<sub>2</sub> plants had latent periods longer than either

parent and as long as that of the very slow-rusting cultivar CI 13227. These results indicate that most of the genes conditioning long latent period in these six cultivars differ from each other and that they show additive effects. Wheats with very long latent periods can be obtained by making crosses among different slow-rusting wheat cultivars.

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

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Slow leaf-rusting is an expression of resistance in wheat (*Triticum aestivum* L. em. Thell) that retards disease progress in the field even though the infection type indicates a compatible interaction between the host and the pathogen, *Puccinia recondita* Rob. ex Desm (1). This resistance has been found and characterized in several cultivars of diverse origin (7,12,15,17). We began using

this resistance in the wheat breeding program at Purdue University several years ago and, at the same time, began studies on its genetic control. The latent period is highly correlated with disease development in the field and is the easiest component of slow-rusting to measure in the greenhouse in monocyclic infection experiments (14,16). Therefore, this component has been used to study the inheritance of slow rusting (8, 10).

We previously reported that in crosses between slow- and fast-rusting wheats, latent period was typically controlled by two to three partially recessive genes that showed additive effects (10). The objective of this study was to determine whether slow leaf-rusting

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cultivars of diverse origin possess unique genes for control of latent period, and if so, whether these genes also show additive effects.

## MATERIALS AND METHODS

Experiments were carried out in the greenhouse with seven populations derived from crosses among six slow leaf-rusting wheat cultivars (S/S crosses). Cultivars CI 13227, Suwon 85, SW 72469-6, L574-1, CI 10745, and Purdue breeding line P65113B6 have been the subjects of earlier reports (10,16). Fast-rusting cultivar Morocco was included as a check.

Seedlings in the one-leaf stage were vernalized in a cold room (3 C) for 8-10 wk and then transplanted individually into 500-ml plastic pots containing standard greenhouse soil mix. Plants were grown in a greenhouse where natural daylight was supplemented with incandescent and fluorescent light, resulting in a total photon flux density on the greenhouse bench of approximately  $167 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  for 16 hr each day from transplanting until maturity.

When a plant reached the preboot to early heading stages of growth, the adaxial surface of the flag leaf was inoculated with urediniospores of culture 7434-1-IT of *P. recondita*. This culture was virulent to all wheat cultivars used in this experiment and was described previously (7). A DeVilbiss atomizer operated at an air pressure of about  $0.35 \text{ kg}\cdot\text{cm}^{-2}$  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 [13]) on susceptible plants. After inoculation, the plants were sprayed lightly with distilled water, kept wet in a moisture chamber for 14-16 hr, and then returned to the greenhouse bench. The mean temperature in the greenhouse was 23 C.

Latent period was calculated by first estimating the proportion of visible infection sites that had developed into uredinia on each flag leaf, beginning 6 days after inoculation and continuing until all the infection sites (flecks) had erupted into uredinia (10). By

regression of the probit of cumulative proportion of uredinia erupted on 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 (14). The methods for analyzing genetic data on length of latent period were the same as described previously (9,10).

## RESULTS

**Suwon 85/L 574-1.** The mean latent periods of Suwon 85 (9.4 days) and L 574-1 (9.7 days) were nearly identical (Fig. 1). The mean latent period of the  $F_1$  plants was shorter than that of either parent, but longer than that of fast-rusting cultivar Morocco. The distribution of latent periods in the  $F_2$  population was continuous and ranged from 6.2 to 18.5 days. The  $F_2$  population showed transgressive segregation in both directions, and its mean latent period was longer than that of either parent. The latent period of fast-rusting Morocco ranged from 5.6 to 6.7 days with a mean of 6.1 days.

**Suwon 85/SW 72469-7.** The mean latent period of SW 72469-7 was 1.7 days longer than that of Suwon 85 and 2 days longer than that of the  $F_1$  of the cross between them (Fig. 2). The distribution of latent periods of  $F_2$  plants was continuous, almost normal, and ranged from 5.9 to 16.6 days, showing transgressive segregation in both directions. Even though the mean latent period of the  $F_1$  plants (8.4 days) was longer than that of the fast-rusting cultivar Morocco, it was shorter than the latent period of either parent.

**Suwon 85/CI 13227.** The mean latent period of CI 13227 was longer than that of Suwon 85 by 2.2 days (Fig. 3). Latent periods of CI 13227 ranged from 10.4 to 13.1 days and those of Suwon 85 ranged from 8.4 to 10.4 days. The mean latent period of the  $F_1$  (8.3 days) was shorter than those of the parents but longer than that of the fast-rusting cultivar Morocco. The latent period distribution of the  $F_2$  population was continuous and showed transgressive segregation. The latent periods of the  $F_2$  population ranged from 7.6 to 21.7 days.

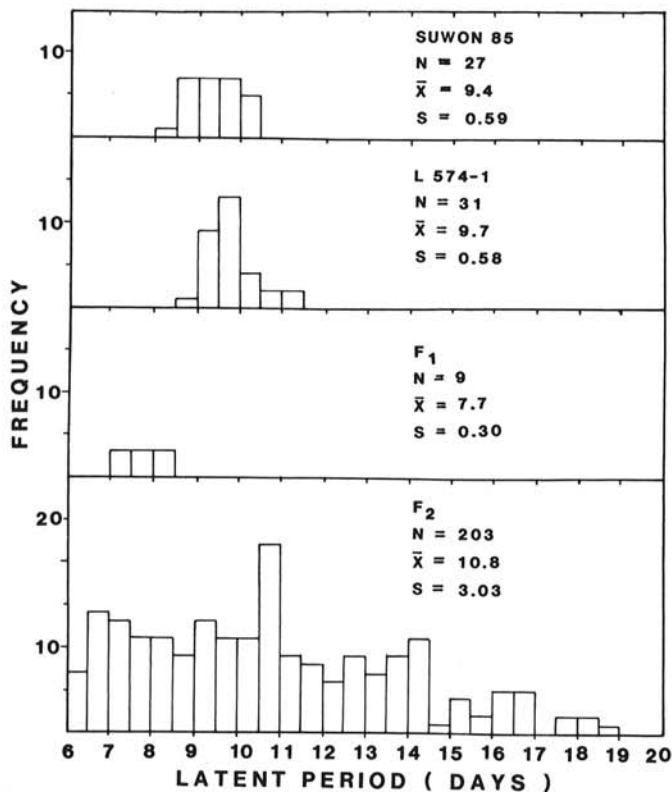


Fig. 1. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 85, L574-1, and the  $F_1$  and  $F_2$  populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

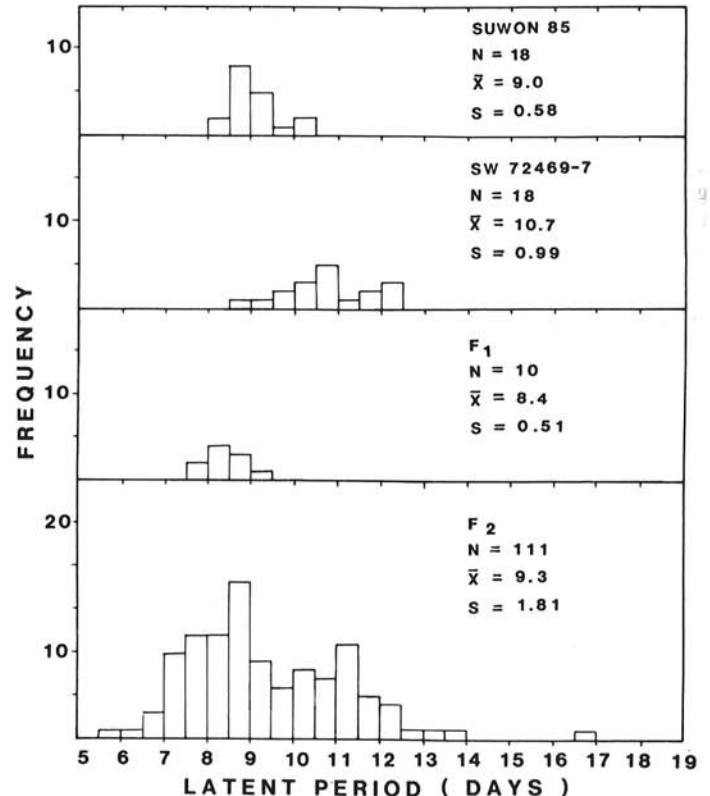


Fig. 2. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 85, SW 72469-7, and the  $F_1$  and  $F_2$  populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

**Suwon 85/CI 10745.** The frequency distributions of latent periods of wheat cultivars Suwon 85, CI 10745, and the  $F_1$  and  $F_2$  populations of the cross between them are summarized in Fig. 4. The distributions of latent periods and the mean latent periods of both parents were almost the same. The mean latent period of the  $F_1$  was a little longer than that of either parent. The latent period distribution of  $F_2$  plants ranged from 5.9 to 14.5 days.

**Suwon 85/P65113B6.** The mean latent period of Suwon 85 was not significantly longer than that of P65113B6 (Fig. 5). Latent periods of Suwon 85 ranged from 8.4 to 10.4 days; those of P65113B6 ranged from 7.9 to 10.3 days. The mean latent period of the  $F_1$  population was 10.8 days with a range of 10.3–11 days. The distribution of latent periods in the  $F_2$  population was continuous, skewed towards a short latent period, and indicated transgressive segregation. A few  $F_2$  plants had exceedingly long latent periods (18 days).

**CI 13227/CI 10745.** The mean latent period of CI 13227 was longer than that of CI 10745 by 4.4 days and the distributions of latent periods of these cultivars did not overlap (Fig. 6). Latent periods of CI 13227 ranged from 11.9 to 14.8 days and those of CI 10745 ranged from 8 to 10.8 days. The mean latent period of  $F_1$  plants (9.1 days) was similar to that of CI 10745. The latent periods of the  $F_2$  population ranged from 6.3 to 16.4 days with a mean of 10.4 days. Thus, the latent periods in some  $F_2$  plants were as short of those of the susceptible wheat cultivar Morocco and some of them were longer than those of CI 13227.

**SW 72469-6/CI 10745.** SW 72469-6 had a mean latent period of 0.9 days longer than that of CI 10745 and 0.3 days longer than that of the  $F_1$  of the cross between them (Fig. 7). The latent period distribution of the  $F_2$  plants showed transgressive segregation in both directions. Several  $F_2$  plants had a much longer latent period than either parent.

## DISCUSSION

The latent period distributions of  $F_2$  populations of all crosses between slow-rusting cultivars were continuous and showed

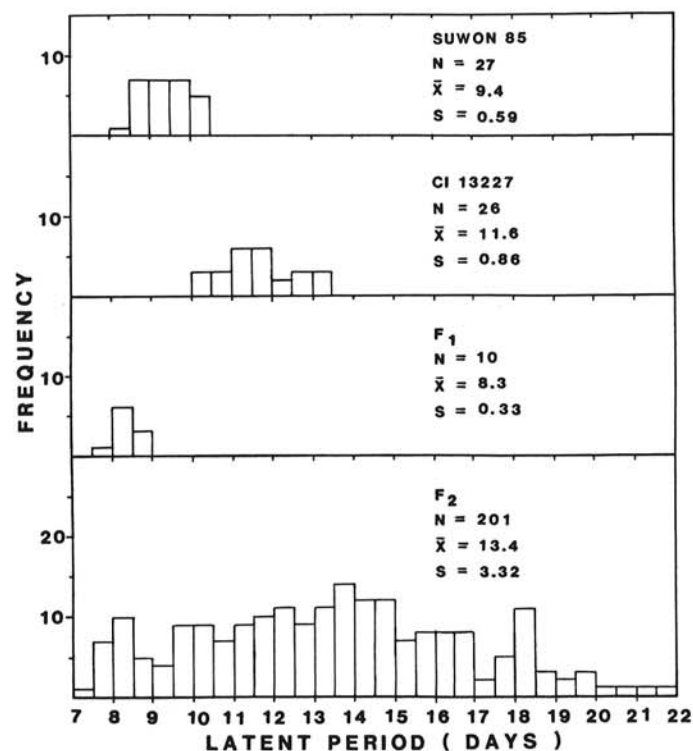


Fig. 3. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 85, CI 13227, and the  $F_1$  and  $F_2$  populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

transgressive segregation toward both shorter and longer latent periods than those shown by the parents. In three of the seven  $F_2$  populations used in this study (Suwon 85/SW 72469-6, Suwon 85/L 574-1, and Suwon 85/CI 13227), the  $F_1$  had a mean latent period shorter than that of either parent, but none of the  $F_1$  plants had a latent period as short as that of Morocco, which has the shortest latent period of any wheat we have studied. Because the long latent periods of these slow-rusting parents are controlled by two or three partially recessive genes with additive effects (8–10), it was expected that latent periods of  $F_1$  progenies of crosses between them would be shorter than latent periods of the parents.

In the cross of Suwon 85/L 574-1, we assumed that the mean effect of genes conditioning long latent period in Suwon 85 was 3.3 days because the mean latent period of Suwon 85 was 9.4 days, i.e., 3.3 days longer than the mean latent period of Morocco. The longest latent period of any of the plants of L574-1 that we tested in experiments with this cross was 11.2 days. Thus, latent periods of  $F_2$  plants longer than 14.5 days ( $11.2 \pm 3.3$  days) would presumably be due to the effects of epistatic or modifying gene actions.

In the cross Suwon 85/CI 13227, the latent period of the  $F_1$  plants was 8.3 days, just 2.2 days longer than that of Morocco, and a little longer than 7.75 days, which is the mean latent period of Morocco plus the effect of one gene from Suwon 85 (1.65 days). The shortest latent periods observed among  $F_1$  and  $F_2$  plants were 7.8 and 7.6 days, respectively. Thus, it is possible that one gene conditioning long latent period is common to both Suwon 85 and CI 13227. Since the longer latent period of CI 13227 is governed by three recessive genes (9), plants with latent periods longer than 16.4 days in the  $F_2$  population might be recovered as a result of epistatic or modifying interactions from both parents. The mean effect of genes governing latent period of Suwon 85 is 3.3 days and the longest period of any CI 13227 parental plant was 13.1 days. Thus, the short latent periods in  $F_1$  plants and the transgressive segregation found in three S/S crosses suggest that the genes for long latent period of the four wheat cultivars are different. Transgressive segregation for resistance has been reported in barley

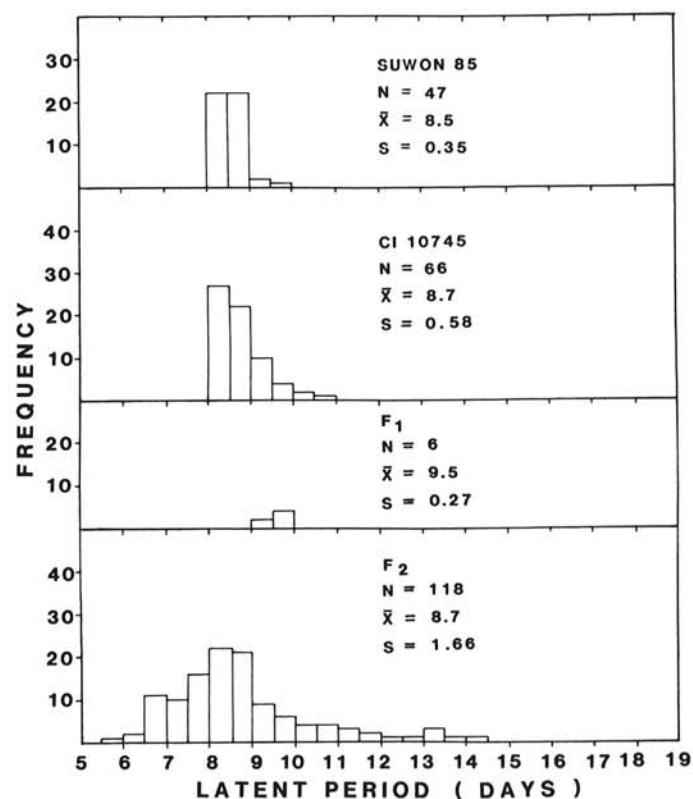


Fig. 4. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 85, CI 10745, and the  $F_1$  and  $F_2$  populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

progenies infected with *P. hordei*, wheat progenies infected with *P. recondita* and *P. graminis* f. sp. *tritici*, corn progenies infected with *P. sorghi*, and potato progenies infected with *Phytophthora infestans* (3,5,6,18,19).

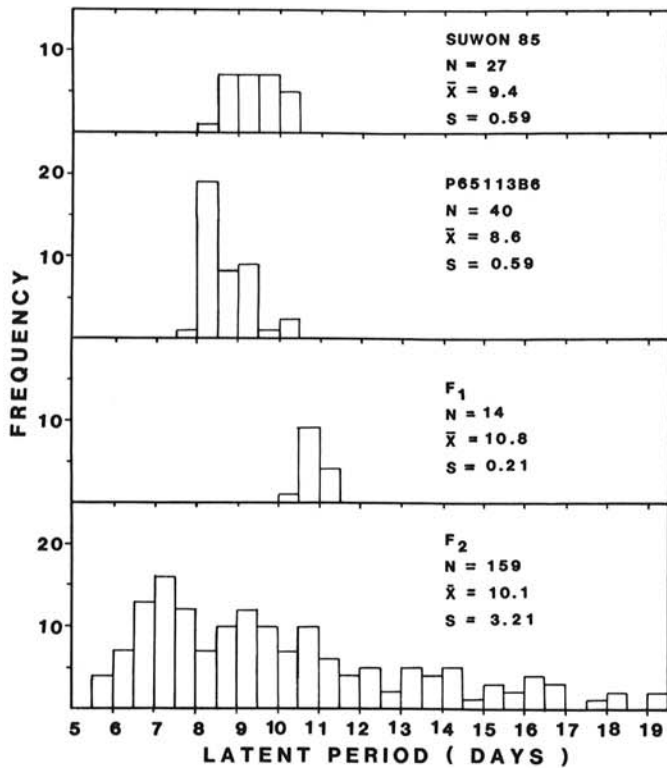


Fig. 5. Frequency distributions of latent periods of leaf rust on wheat cultivars Suwon 85, P65113B6, and the F<sub>1</sub> and F<sub>2</sub> populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

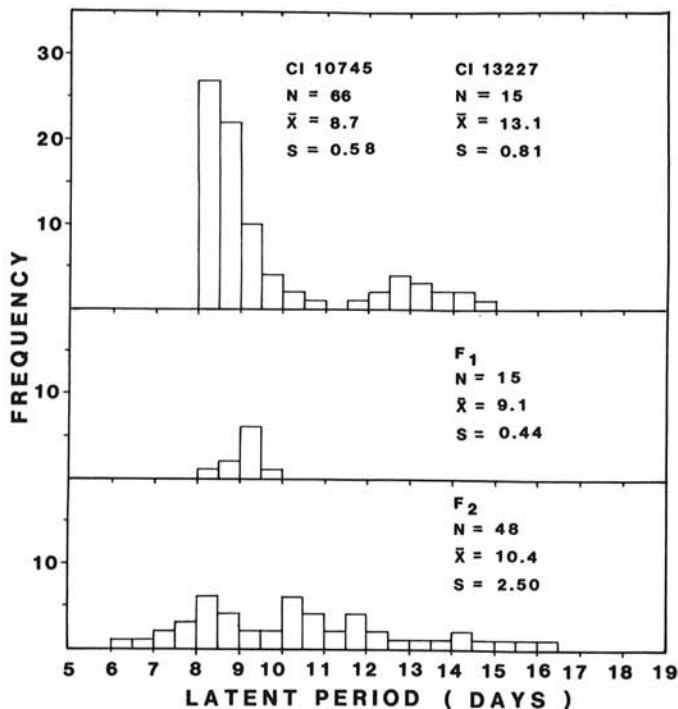


Fig. 6. Frequency distributions of latent periods of leaf rust on wheat cultivars CI 10745, CI 13227, and the F<sub>1</sub> and F<sub>2</sub> populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

Four of the seven F<sub>2</sub> populations used in this study (Suwon 85/P65113B6, SW 72469-6/CI 10745, Suwon 85/CI 10745, and CI 13227/CI 10745) have shown not only transgressive segregation toward both shorter and longer latent periods than those of the parents, but also their F<sub>1</sub> mean latent periods were almost the same or longer than those of their parents. Because the genes conditioning the long latent periods of these slow-rusting cultivars are recessive and oligogenic (9,10), it was not expected that latent periods of F<sub>1</sub>s would be equal to or longer than those of their parents. A similar result was reported by Lupton and Macer (11) working with the wheat cultivar Minister, which is resistant to five races of *Puccinia striiformis*. Minister appeared to have a single recessive gene for resistance to race 2B when the F<sub>2</sub> population of the cross between Minister and susceptible cultivar Holdfast was inoculated. Inoculation of the F<sub>2</sub> of Minister/Cappelle with the same race 2B indicated that a single dominant gene conferred resistance. Wheat cultivar Cappelle was susceptible to race 2B and resistant to four other races, but Holdfast was susceptible to all five races. The reason for the reversal of resistance from recessive to dominant was that F<sub>2</sub> heterozygous plants of Minister/Holdfast were susceptible but heterozygous plants of Minister/Cappelle were resistant. Macer and Lupton (11) postulated that even though the gene *Yr3a* carried by Cappelle was not able to confer resistance to race 2B, the presence of this gene in a heterozygous condition could increase the effect of gene *Yr3c*, which is carried by Minister. This experiment showed that even though wheat cultivar Cappelle is fully susceptible to race 2B, its genetic background could give an increased level of resistance to race 2B in the heterozygous state. Dyck and Samborski (2) reported that leaf rust resistance in wheat cultivar Loros, which behaved as a dominant or partially dominant trait in a cross with susceptible cultivar Red Bobs, behaved as a recessive trait in a cross with another susceptible cultivar, Thatcher. This suggests that a modifying factor (gene) within a susceptible cultivar could reverse the dominance of resistance to recessiveness. Johnson and Wilcoxson (5) reported that very slow-rusting lines were recovered from F<sub>5</sub> families of certain fast-rusting/fast-rusting

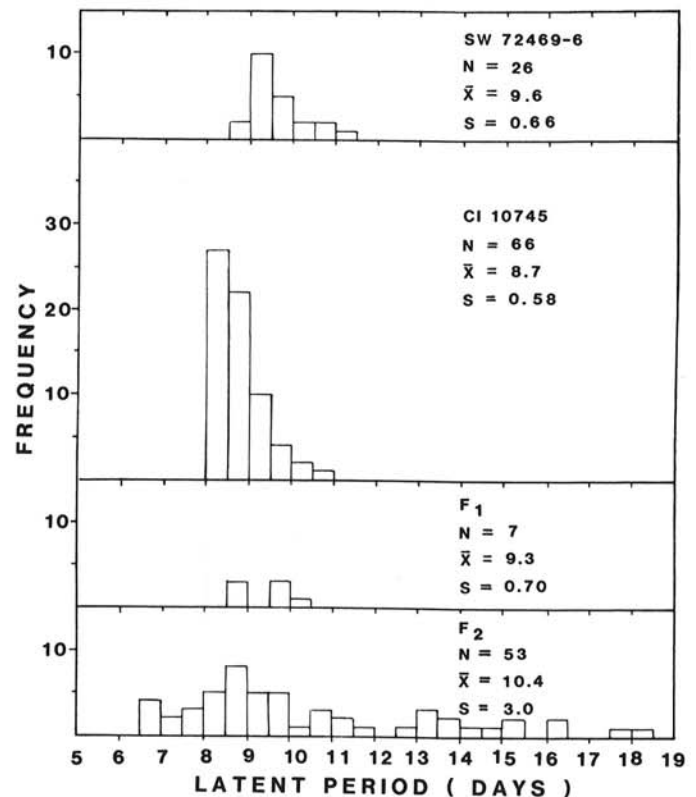


Fig. 7. Frequency distributions of latent periods of leaf rust on wheat cultivars SW 72469-6, CI 10745, and the F<sub>1</sub> and F<sub>2</sub> populations of crosses between them ( $N$  = number of plants,  $\bar{X}$  = population mean (days), and  $S$  = population standard deviation).

crosses of barley infected with *P. hordei*. Their report suggested that even barley cultivars very susceptible to *P. hordei* may possess modifying genes that give rise to higher levels of resistance in crosses with other susceptible barley cultivars. Thus, the longer latent periods in the F<sub>1</sub> and transgressive segregations in four F<sub>2</sub> populations of crosses between slow-rusting cultivars may be due to modifiers, epistasis, or complementation in the heterozygous state.

Hughes and Hooker (4) reported that increased general resistance to northern corn leaf blight was recovered from corn hybrid combinations that have unrelated parental sources of resistance. In all of our crosses, some F<sub>2</sub> progeny had much longer latent periods than their parents. From the crosses between unrelated wheats such as Suwon 85/P65113B6, about 50% of the F<sub>2</sub> plants showed transgressive segregation toward a longer latent period. However, from the cross between the related Suwon 85 and SW 72469-6, only about four of 111 plants had a latent period longer than SW 72469-6, the parent with the longer latent period.

Transgressive segregation toward longer latent periods also indicates that different genes for slow rusting resistance from different sources show additive effects. Thus, we should be able to develop greater levels of slow rusting by intercrossing diverse slow-rusting cultivars. The levels of slow rusting available in the parental cultivars can reduce leaf rust progress greatly (16). Even greater levels may reduce rust progress to a negligible degree and provide durability of resistance.

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