

Inheritance of Field Weathering Resistance in Soybean [*Glycine max* (L.) Merrill]

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ABSTRACT

A commercial variety of soybean, Chiangmai 60, which is susceptible to field weathering and two field weathering resistant varieties, GC 10848 and Kalitur, were grown and hybridized in the greenhouse at the Department of Agronomy, Kasetsart University. The F₁ hybrid seeds and their parental varieties were planted in the greenhouse to produce F₂ seeds. Parental varieties, F₁ hybrids and F₂ progenies were grown in an experimental field during the 2008 dry season at the National Corn and Sorghum Research Center, Pakchong District, Nakhon Ratchasima province. Individual plots were 3×3 m², with six rows, composed of two rows of parents and four rows of F₁ hybrids or F₂ progenies for each cross. The spacing between rows was 50 cm and between hills was 25 cm. At physiological maturity, soybean pods were harvested, threshed and subjected to tests for accelerated aging (AA) and electrical conductivity (EC), and the seed coat percentage was measured. Field weathering resistance of the parental plants, F₁ hybrids and F₂ progenies was evaluated using germination percentages after AA testing and EC values of seed leachate and seed coat percentages. Dominance percentages of F₁ hybrids and the frequency distribution of F₂ progenies for the germination percentages after AA testing and EC values of seed leachate and seed coat percentages of the two soybean crosses revealed that field weathering resistance was controlled by a polygene with partial dominance.

Keywords: soybean, inheritance, field weathering, seed vigor, accelerated aging test, electrical conductivity test

INTRODUCTION

Historically, soybean has been produced in the northern regions of the world's temperate climatic zone, where environmental stresses are relatively minimal. However, as the world demand for vegetable oil and protein has continued to

increase, soybean production has spread rapidly into the hot and humid areas, and more recently into the tropical regions (Moore, 1966). A major constraint to the expansion of soybean production into the tropics is the difficulty of producing high quality seed. Tropical conditions, involving high temperature and relative humidity during the seed

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maturation period, are not conducive to the production of high quality seed, which is necessary to establish acceptable crops (Paschal and Ellis, 1978). Soybean seeds deteriorated faster than the seed of most other crops, especially under tropical conditions (Priestley *et al.*, 1985). The process of deterioration in seed quality that occurs between the stages of post-maturation and pre-harvest is referred to as field weathering (TeKrony *et al.*, 1980a).

Field weathering of soybean seeds can be minimized by enhancing field management, such as by carefully matching the maturity of the cultivar with rainfall patterns (Franca Neto *et al.*, 1994), choosing a suitable latitude of the specific seed production region (TeKrony *et al.*, 1980b) and using foliar fungicides and defoliant (Franca Neto *et al.*, 1984). In addition, using a field weathering resistant variety can reduce seed deterioration. Specifically, a field weathering resistant variety allows farmers to grow soybean in both rainy and dry seasons (Wien and Kueneman, 1981). Varietal differences have been identified for resistance to field weathering and deterioration during storage (Ndimande *et al.*, 1981).

Choosing a resistant variety is the most important and essential way to solve the field weathering problem. Generally, field weathering resistant varieties are low in grain yield and market demand. The hard seed coat that can contribute to field weathering resistance is not desired as commercial seed, because of non-uniform germination and emergence. Small seed size and a black seed coat for field weathering resistance are also not favored in the market, even though they have no influence on yield. Special care is needed when using these characteristics in a breeding program (Hill *et al.*, 1986).

At present, field weathering breeding is limited by the lack of genetic information. Inheritance of field weathering resistance should be investigated to facilitate the breeding process

for improving field weathering resistant varieties. Only a small amount of work has been done on the inheritance of field weathering resistance, such as the research by Unander *et al.* (1983), Dechkrong (2006) and Changrong *et al.* (2006, 2007). However, their work was not detailed. Therefore, it is necessary to study the inheritance of field weathering resistance of soybean for future breeding programs. The objective of this study was to determine the inheritance of field weathering resistance in some soybean varieties.

MATERIALS AND METHODS

Planting the parental varieties and making crosses to produce F₁ hybrids

Chiangmai 60 (CM60), which is susceptible to field weathering (Kaowanant, 2003) and two field weathering resistant varieties, GC 10848 and Kalitur (Yupongchay, 2008), were grown in the greenhouse at the Department of Agronomy, Kasetsart University. Susceptible female parents were emasculated and hybridized with two resistant parents for two cross combinations, following the method described by Poehlman and Sleper (1995).

Production of F₂ seeds

The F₁ hybrid seeds were planted in the greenhouse to produce F₂ seeds. The F₁ plants were identified as real hybrids using hypocotyl color and flower color as morphological markers, as described by Bernard and Weiss (1973).

Field test

Parents, F₁ hybrids and F₂ progenies were grown in an experimental field during the 2008 dry season at the National Corn and Sorghum Research Center, Pakchong District, Nakhon Ratchasima province. Individual plots were 3×3 m², with six rows, composed of two rows of parents and four rows of F₁ hybrids or F₂ progenies for each cross. The spacing between

rows was 50 cm and between hills was 25 cm. At physiological maturity, the yellow pods were harvested from each plant of parents, F₁ hybrids and F₂ progenies for field weathering testing. At this stage, about 95% of the pods were yellow, but had not turned brown (Dassou and Kueneman, 1984). This stage was approximately R7.5, as described by Horlings *et al.* (1994).

Field weathering test

The yellow pods harvested from each plant of parental varieties, F₁ hybrids and F₂ progenies were air dried to approximately 12% moisture content and hand threshed. The seeds obtained were subjected to the following field weathering tests.

Accelerated aging test

Twenty-five seeds from each plant of parents (30, 30 and 30 plants), F₁ hybrids (10 and 30 plants) and F₂ progenies (239 and 359 plants) of the two crosses were put on wire-mesh trays. The trays were each sealed in a plastic box with 1 cm depth of water under the tray to ensure a high relative humidity (90-100%) during incubation. The boxes were then incubated at 41°C for 3 d (AOSA, 1983). The treated 25 seeds were germinated between wet paper at 25°C for 5 d. The normal seedlings, abnormal seedlings, fresh un-germinated seeds, hard seeds and dead seeds were counted. Germination percentage was calculated, according to ISTA (1985).

Electrical conductivity test

Twenty-five seeds from each plant of parents (30, 30 and 30 plants), F₁ hybrids (10 and 30 plants) and F₂ progenies (239 and 359 plants) of the two crosses were weighed and soaked in 75 ml distilled water in a 200-ml beaker. A control treatment was used by adding only 75 ml of distilled water into the 200-ml beaker. The beakers were covered with aluminum foil and incubated at 20°C for 24 h (AOSA, 1983). Then, the electrical conductivity of the seed leachate was measured by a Cyberscan pc 510 digital meter and recorded in micro Siemen (μS) per cm per gram of seed.

Measurement of seed coat percentage

Ten seeds from each plant of parents (30, 30 and 30 plants), F₁ hybrids (10 and 30 plants) and F₂ progenies (239 and 359 plants) of the two crosses were soaked in distilled water and incubated at 5°C for 15-16 h. The seed coat was separated from the seed using a razor blade. The seed (without its seed coat) and seed coat were dried in a hot air oven at 105°C for 24 h. After drying, the seed and seed coat were weighed and the seed coat percentage was calculated (Kuo, 1989).

Genetic analysis

Field weathering resistance of soybean seeds from each plant of parents, F₁ hybrids and F₂ progenies of the two crosses was evaluated using the germination percentage after AA testing, the EC value of seed leachate and the seed coat percentage. The mean, standard error and the frequency distribution for these three parameters were calculated for the parents, F₁ hybrids and F₂ progenies. Mid-parent values and dominance percentages of the two crosses for the three parameters were also calculated and all the data were analyzed using the following formulas:

$$\text{Mid-parent (MP)} = \frac{\bar{P}_1 - \bar{P}_2}{2} \text{ and dominance percentage} = \frac{\bar{F}_1 - \text{MP}}{\text{MP}} \times 100$$

RESULTS AND DISCUSSION

Field weathering resistance manifested by germination percentage

In the AA test, germination after aging was closely related to field emergence under adverse conditions (Delouche and Baskin, 1973). The two environmental variables in the AA test (high temperature and high humidity) caused rapid deterioration of the exposed seeds. High vigor seed lots can withstand these extreme stress conditions and deteriorate at a slower rate than low vigor seed lots (AOSA, 1983). The AA test is one of the most

frequently used for seed vigor evaluation. The seed lots with high germination percentages had high seed vigor, whereas those with low germination percentages had low seed vigor (Ferguson *et al.*, 1990). Dassou and Kueneman (1984) reported that soybean genotypes with high germination percentages following weathering treatment were resistant to field weathering. Egli and TeKrony (1995) indicated that soybean seed lots with higher germination rates after AA testing manifested a high probability of producing adequate seedling emergence under severe environmental conditions. Furthermore, Marwanto (2003) reported that germination after weathering stress positively correlated with soybean seed quality. Phan *et al.* (2006) evaluated soybean lines and found that those with higher percentages of seed germination following AA testing were resistant to field weathering.

In this study, the range and mean of susceptible (CM60) and resistant (GC 10848 and Kalitur) parental varieties, F₁ hybrids and F₂ progenies of the two soybean crosses for germination percentages after AA testing were calculated (Table 1). Mid-parent values and dominance percentages were also determined. The mean germination percentages of CM60, GC 10848 and Kalitur were 43.20, 88.80 and 86.67%, respectively. Resistant parental varieties showed more than double the germination percentages of the susceptible varieties. For the CM60 × GC 10848 cross, the mean germination percentage of

the F₁ hybrid and mid-parent value were 70 and 66%, respectively, whereas the germination percentages of F₂ segregating progenies ranged from 33 to 100%, with a mean value of 68.13%. For the CM60 × Kalitur cross, the mean germination percentage of the F₁ hybrid and mid-parent value were 69.23 and 64.93%, respectively, whereas the germination percentages of F₂ segregating progenies varied from 32 to 100%, with a mean value of 67.28%.

The frequency of the germination percentages of F₂ segregating progenies of both crosses showed a continuous distribution and normal curves (Figures 1a and 1b). Therefore, the field weathering resistance in soybean identified by germination percentages after AA testing was controlled by a polygene. Furthermore, the mean germination percentages of the F₁ hybrids of both crosses were intermediate between the parents and higher than the mid-parent value (Table 1). The dominance percentages of both crosses were 6.06 and 6.62%, which revealed that there was partial dominance of resistance to field weathering. The result was the same as the findings of Dechkrong (2006) and Changrong *et al.* (2006, 2007), who reported that field weathering resistance of soybean appeared to be a quantitative trait controlled by a polygene. Unander *et al.* (1983) considered that, like some other environmental stress resistance factors in plants, field weathering resistance of soybean may also be controlled by a polygene.

Table 1 Range and mean (±standard error) for germination percentages after AA testing of parental varieties, F₁ hybrids and F₂ progenies in the two crosses of soybean.

Population	CM60 × GC10848		CM60 × Kalitur	
	Range	Mean ± S.E.	Range	Mean ± S.E.
P ₁	24 - 60	43.20 ± 1.78	24 - 60	43.2 ± 1.78
P ₂	82 - 100	88.80 ± 1.03	82 - 94	86.67 ± 0.65
F ₁	65 - 75	70.00 ± 1.29	57 - 81	69.23 ± 1.26
F ₂	33 - 100	68.13 ± 1.02	32 - 100	67.28 ± 0.84
Mid-parent		66.00		64.93
Dominance (%)		6.06		6.62

Field weathering resistance identified by electrical conductivity value

The electrical conductivity (EC) of seed leachate has been used satisfactorily to determine the vigor of soybean seed (AOSA, 1983). Hampton and TeKrony (1995) reported that the membrane structure and cell leachate were usually associated with seed vigor. Highly vigorous seeds could re-establish their membrane integrity at a faster rate with less leachate (lower EC value) than those with low vigor. Furthermore, Chanprasert *et al.* (1996) found that the EC value of the seed leachate was correlated with seed quality, which included seed vigor during field deterioration (weathering). Phan *et al.* (2006) evaluated soybean lines with low EC values of seed leachate (higher seed vigor) and found that they were resistant to field weathering. Dechkrong (2006) reported that the F₂ segregating progenies with low EC values were resistant, while those with high EC values were susceptible to field weathering. Win *et al.* (2009) demonstrated that soybean varieties/lines with lower EC values of seed leachate tended to be more resistant to field weathering.

In the current study, the range and mean EC values of seed leachate were analyzed for parents, F₁ hybrids and F₂ progenies of the two soybean crosses. Mid-parent values and dominance percentages were also calculated. The mean EC value of CM60, GC 10848 and Kalitur was 131.40, 78.05 and 85.20 $\mu\text{S/cm/g}$ seed, respectively (Table 2). The EC values of resistant

parent had much lower EC values than those of the susceptible parents. For the CM60 $\times$ GC 10848 cross, the mean EC values of F₁ hybrids and mid-parent value were 113.99 and 104.72 $\mu\text{S/cm/g}$ seed, whereas the EC values of F₂ progenies ranged from 70.82 to 146.49 $\mu\text{S/cm/g}$ seed with a mean value of 109.28 $\mu\text{S/cm/g}$ seed. For the CM60 $\times$ Kalitur cross, the mean EC values of F₁ hybrids and mid-parent were 119.04 and 108.30 $\mu\text{S/cm/g}$ seed, whereas the EC values of F₂ progenies varied from 62.33 to 150.09 $\mu\text{S/cm/g}$ seed, with a mean value of 113.65 $\mu\text{S/cm/g}$ seed.

The frequency of the EC values of F₂ progenies of both crosses was also continuously distributed and had a normal curve (Figures 1c and 1d) suggesting that field weathering resistance in soybean evaluated by EC value was controlled by a polygene. Table 2 demonstrates that in the CM60 $\times$ Kalitur cross, the lowest EC value of some F₂ progenies (62.33 $\mu\text{S/cm/g}$ seed) was lower than that of the resistant parent, Kalitur (74 $\mu\text{S/cm/g}$ seed) and the highest EC value of some F₂ progenies (150.09 $\mu\text{S/cm/g}$ seed) was higher than that of the susceptible parent, CM60 (140 $\mu\text{S/cm/g}$ seed). This revealed that the character in this cross had transgressive segregation. This finding was consistent with the report of Dechkrong (2006) that field weathering resistance expressed by EC value was monitored by a polygene with transgressive segregation in F₂ progenies. Moreover, Table 2 also shows that the mean EC values of F₁ hybrids were intermediate between

Table 2 Range and mean ($\pm$ standard error) for EC values of seed leachate ($\mu\text{S/cm/g}$ seed) of parental varieties, F₁ hybrids and F₂ progenies in the two crosses of soybean.

Population	CM60 $\times$ GC10848		CM60 $\times$ Kalitur	
	Range	Mean $\pm$ S.E.	Range	Mean $\pm$ S.E.
P ₁	123.00 - 140.00	131.40 $\pm$ 0.92	123.00 - 140.00	131.40 $\pm$ 0.92
P ₂	64.09 - 91.09	78.05 $\pm$ 1.34	74.00 - 94.00	85.20 $\pm$ 1.21
F ₁	105.49 - 123.49	113.99 $\pm$ 2.20	105.31 - 130.31	119.04 $\pm$ 1.39
F ₂	70.82 - 146.49	109.28 $\pm$ 0.77	62.33 - 150.09	113.65 $\pm$ 0.70
Mid-parent	104.72		108.30	
Dominance (%)	8.85		9.92	

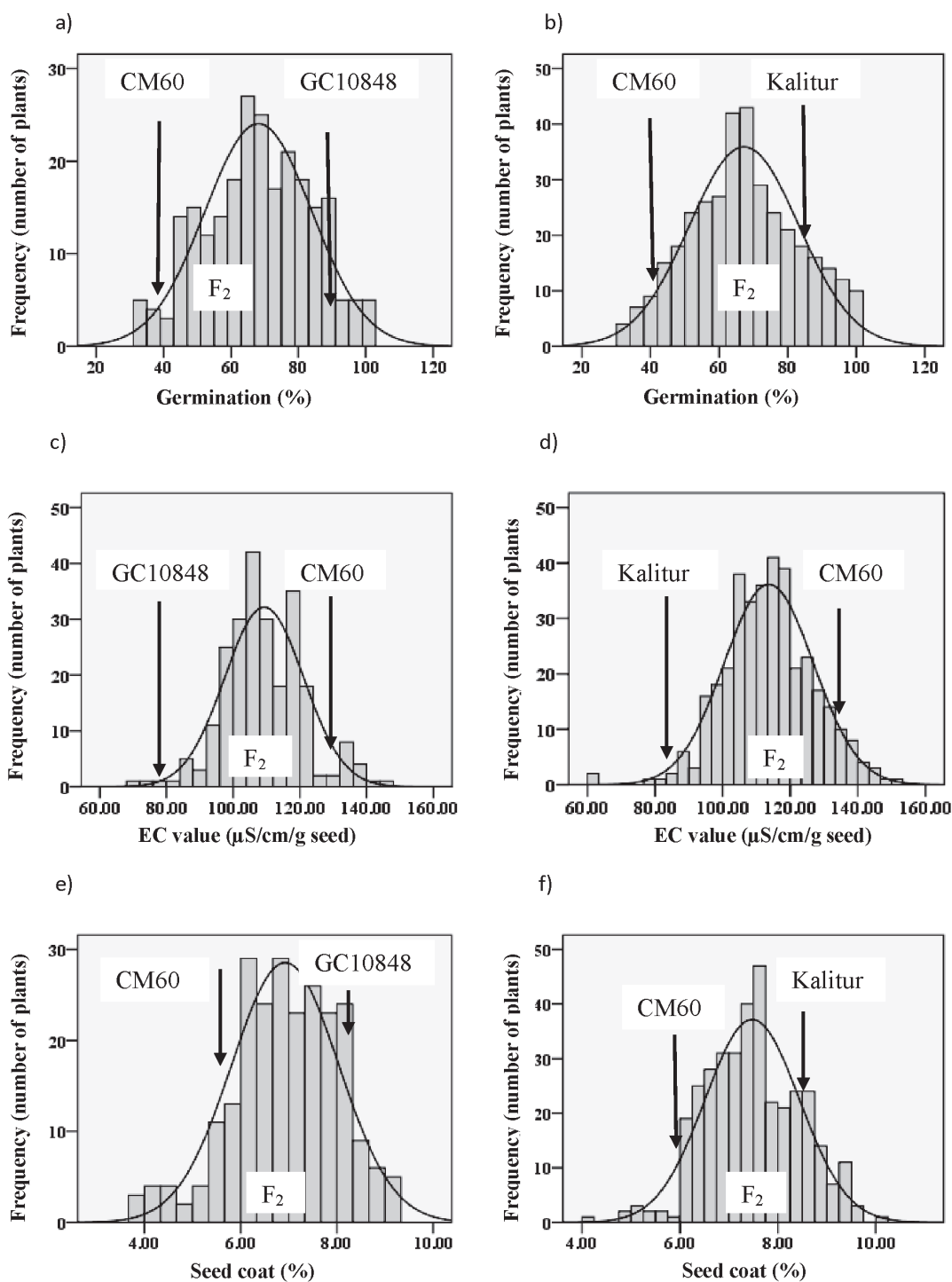


Figure 1 Frequency distribution of parental varieties and F_2 progenies of the two crosses of soybean CM60 $\times$ GC10848 and CM60 $\times$ Kalitur for germination percentages after AA test (a, b); EC values of seed leachate (c, d); and seed coat percentages (e, f).

those of parents and higher than the mid-parent value. The dominance percentages of both crosses were 8.85 and 9.92%, which implied partial dominance of susceptibility to field weathering. The partial dominance of susceptibility to field weathering might be affected by the maternal (CM60) tissue. Kilen and Hartwig (1978) studied the heritability of an impermeable seed coat and its association with EC value and concluded that the trait was controlled by maternal tissue, which supported the findings of the current study.

Field weathering resistance revealed by seed coat percentage

Kuo (1989) reported that soybean seed possessing higher specific weight of the testa showed lower membrane permeability. Consequently, high seed vigor of soybean lines might have resulted from the delayed permeability of the seed coat when the seeds were exposed to field weathering. This finding opens up the possibility of breeding soybean for resistance to field weathering by increasing the proportion of seed coat. Chanprasert *et al.* (1996) found that seed coat percentage and seed weight were correlated with seed quality during field deterioration (weathering). Phan *et al.* (2006) identified that the field weathering resistant soybean lines having high seed germination and vigor exhibited higher seed coat percentages than the susceptible ones. Dechkrong (2006) reported that F_2 progenies having high seed coat percentages tended to be

more resistant to field weathering than the ones with low seed coat percentages. Win *et al.* (2009) also found that soybean genotypes with low seed weight tended to have high seed coat percentage, which caused greater resistance to field weathering.

In the present study, the range and mean of seed coat percentage for parents, F_1 hybrids, F_2 progenies of the two soybean crosses are shown in Table 3. Mid-parent values and dominance percentages were also determined. The mean seed coat percentages of CM60, GC 10848 and Kalitur were 5.99, 7.60 and 8.34%, respectively. This indicated that resistant parent had higher seed coat percentages than susceptible parents. For the CM60 $\times$ GC 10848 cross, the mean seed coat percentage of F_1 hybrids and the mid-parent value were 7.20 and 6.79 %, whereas the seed coat percentages of F_2 progenies ranged from 3.70 to 9.30%, with a mean value of 6.92%. For the CM60 $\times$ Kalitur cross, the mean seed coat percentage of F_1 hybrids and the mid-parent value were 7.88% and 7.16, while seed coat percentages of F_2 progenies varied from 4.20 to 10.10%, with a mean value of 7.47%.

The frequencies of the seed coat percentages of F_2 progenies of both crosses were continuously distributed and had a normal curve (Figures 1e and 1f), suggesting that field weathering resistance in soybean manifested by seed coat percentage was controlled by a polygene. Furthermore, the mean seed coat percentages of

Table 3 Range and mean ($\pm$ standard error) for seed coat percentages of parental varieties, F_1 hybrids and F_2 progenies in the two crosses of soybean.

Population	CM60 $\times$ GC10848		CM60 $\times$ Kalitur	
	Range	Mean $\pm$ S.E.	Range	Mean $\pm$ S.E.
P ₁	5.20 - 6.90	5.99 $\pm$ 0.09	5.20 - 6.90	5.99 $\pm$ 0.09
P ₂	6.90 - 8.20	7.60 $\pm$ 0.06	7.40 - 9.50	8.34 $\pm$ 0.12
F ₁	6.60 - 7.80	7.20 $\pm$ 0.11	7.40 - 8.50	7.88 $\pm$ 0.06
F ₂	3.70 - 9.30	6.92 $\pm$ 0.07	4.20 - 10.10	7.47 $\pm$ 0.05
Mid-parent		6.79		7.16
Dominance (%)		6.04		10.05

F₁ hybrids were intermediate between those of parents and higher than the mid-parent value. The dominance percentages of both crosses were 6.04 and 10.05% (Table 3), which revealed partial dominance of resistance to field weathering. Moreover, in both crosses, the lowest seed coat percentages of F₂ progenies (3.70 and 4.20%) were lower than that of the susceptible parent CM60 (5.20%) and the highest seed coat percentages of F₂ progenies (9.30 and 10.10%) were higher than those of the resistant parents, GC 10848 (8.20%) and Kalitur (9.50%). This implied that the character had transgressive segregation. The same result was reported by Dechkrong (2006).

CONCLUSION

Dominance percentages of F₁ hybrids and the frequency distribution of F₂ progenies for germination percentages after AA testing, EC values of seed leachate and seed coat percentages of the two soybean crosses revealed that field weathering resistance was controlled by a polygene with partial dominance.

To improve field weathering resistant varieties, selection can be carried out effectively from segregating progenies of the cross between a susceptible and resistant variety by pedigree or the single seed descent method. Emphasis in selection should be on field weathering resistant characters, including seed germination percentage after AA testing, the EC value of seed leachate and the seed coat percentage in the F₂-F₅ generations. From the F₃ generation onwards, the performance of soybean plants/lines on good agronomic characters can be considered depending on the nature of responsible characters.

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