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Estimation of Heritability and Combining Ability for Fire Blight Resistance in Pear[1]

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Abstract. **Heritability estimates for fire blight resistance in pear were obtained by regressing progeny means on midparental phenotypes. Approximately half of the variability in resistance in pear was additive ($h^2 = 0.52$), but there was also evidence for nonadditive genetic effects compatible with a proposed qualitative gene for sensitivity. A method was established to estimate relative average combining ability for fire blight resistance. Progeny means of individual parents were adjusted to the grand progeny mean of 8 intercrossed testers based on common progeny.**

Resistance to fire blight, caused by the bacterium *Erwinia amylovora* (Burrill) Winslow et al., is a major objective of various pear breeding programs in North America. The expression of resistance depends on interactions between the pathogen, host, and environment. Considerable variability in resistance exists, both within and between species (6, 17, 18, 23). Previous studies have suggested that resistance is controlled by both quantitative and qualitative factors. Evidence for dominant factors for both resistance (14, 21) and sensitivity (20) have been postulated, and numerous studies have noted considerable variability between parents in their ability to transmit resistance to their offspring (14, 15, 21, 23).

Estimation of heritability and combining ability are related techniques that describe the nature of genetic variability in a population and that are useful for selection of parents and of breeding systems. Estimates of heritability of horticulturally important traits have been obtained in various fruit and nut crops, including sweet cherry (8), peach (11), walnut (9), strawberry (4, 7, 10, 16), and plum (12). In pears, however, genetic studies of fire blight resistance have been based principally upon analysis of segregation data. The objective of this study was to apply quantitative analysis of breeding records to 1) estimate heritability for fire blight resistance within a pear breeding population, and 2) to estimate relative average combining abilities of cultivars and selections used as parents.

Materials and Methods

The population. The present study is based upon the breeding records of the USDA pear breeding program at Beltsville, Maryland (5), and is restricted to those progenies planted in the years 1962 through 1966 (2). The crosses were made for the purpose of genetic improvement and are without experimental design. The parents were selected nonrandomly on the basis of their possession of some desirable trait. Although progenies planted each year constitute essentially unique sets of crosses, leading to confounding of genotypic and environmental effects on the expression of fire blight resistance, preliminary studies (1, 2) indicated that under the natural epiphytotic conditions in the orchard, the incidence (% of trees with symptoms) and severity (mean fire blight score) for each year's planting reached comparable and stable levels after 7 years. The data are, therefore, considered to give reasonable estimates of inherent and differential levels of fire blight resistance.

The population studied consisted of progeny from 256 crosses. Reciprocal and repeated crosses were pooled for analysis. (The few progenies of selfs were excluded.) A minimum progeny size (n=11) for estimation of a mean was established, using Stein's 2-stage procedure (19). Relatively large values of d (1.0) and α (0.20) were chosen in order to include as many progenies as possible in the analysis. The parental population included 30 cultivars and 52 advanced selections. Each parent

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was classified according to species background and each cross was classified according to the species pedigree of the parents. A summary of the population is given in Table 1. Although several parents were widely used, the disproportion of parental representation in crosses was not considered to be sufficient to seriously bias estimates of heritability for the entire breeding population.

Evaluation of fire blight. Resistance of seedlings to fire blight was evaluated yearly under natural orchard conditions until seedlings were 7 to 9 years old, allowing the level of fire blight in the orchard to stabilize. Seedlings were scored according to the USDA system, which is based upon the age of the wood infected and a total percentage of the tree blighted (22). A numerical scale represents progressively higher levels of resistance, with a score of 1 corresponding to death from the disease and a score of 10 were included only if they had flowered, since previous data suggested that the onset of flowering is correlated with the occurrence of infection (R. H. Zimmerman, unpublished).

Parental blight phenotypes. Evaluations of 76 parents were based upon data from 3 USDA trials and on 2 published estimates based upon the same data (20, 23). Cultivar and advanced selections were planted from 1960 through 1966 and were evaluated for periods of 6 to 11 years under natural epiphytotic conditions. Because all parents were not evaluated concurrently nor represented in each evaluation, the relative resistance of phenotypes were established by indirect comparison to parents common to each evaluation. Three parents, 'Bartlett', 'Magness', and 'Moonglow', were regarded as standards for comparison. The phenotypic ratings of parents not common to all evaluations were adjusted on the basis of their performance relative to the mean of the 3 standards in each trial, according to the following formula, derived from Janick (13):

$$\overset{\wedge}{\overline{P}}_i = \sum_{j \Box J} \left(\frac{\overline{A}_{ij}}{\overline{B}_j} \times \overline{G}\right) \div n(J_i)$$

where,

$\overline{P}_i$ = adjusted mean phenotype of the ith parent;
$\overline{A}_{ij}$ = mean phenotypic score of the ith parent in the jth trial;
$\overline{B}_j$ = mean of the standard parents on the jth trial;
$\overline{G}$ = grand mean of the standard parents in all trials;
J_i = that set defining those trials in which the ith parent occurred;
$n(J_i)$ = number of trials in which the ith parent occurred;
$j \Box J$ = j takes on those integer values corresponding to the trials in set J.

An example is given in Table 2.

Estimation of heritability. Heritability was estimated by regression of progeny means on mid-parental adjusted phenotype (3), using, as follows:

1. all progenies, $n = 227$;
2. within species cross. Only those species crosses for which the number of crosses exceeded 10 were included in this report;
3. within all crosses involving 'Bartlett';
4. within various crosses involving sensitivity genotypes (*Sese* or *sese*) assigned by Thompson et al. (20), for all progenies and within *Pyrus communis* L. crosses.

The significance of the differences between various regression coefficients was tested by a t-test (19).

Parental prepotency. Relative average combining abilities were computed from mean progeny fire blight scores as a measure of parental prepotency for transmission of resistance. Because all combinations of crosses between parents had not been made and because all parents had not been crossed to a common tester, there was no direct way to compare the average combining abilities for fire blight resistance of all parents. Therefore, a method based upon indirect comparisons through an elite group of tester parents was utilized.

Progeny records were searched to establish a group of parents which had been crossed in all combinations (a diallel). Such a group, designated the standard parents, was found, and consisted of 'Bartlett', 'Magness', 'Moonglow', and 'Kieffer'. (Selfs of 'Moonglow' were excluded, and reciprocals were combined). Because this group was small, a second group was found consisting of US 301, US 307, US 539, and 'Bradford', which had all been crossed to each of the 4 standard parents. The mean blight rankings of 'Bartlett', 'Kieffer', 'Magness', 'Moonglow', US 301, US 307, US 539, and 'Bradford' constituted a set designated as the "elite" group. The appropriate base means (the 4 standard parent means and the mean of US 301, US 307, US 539, and 'Bradford' crossed with 'Bartlett', 'Kieffer', 'Mag-

Table 1. Summary of pear breeding population.

Pyrus species cross	Total no. crosses	Total no. parents	Major parents (no. of crosses)
communis x *communis*	99	53	Magness (22), Moonglow (18), Bartlett (14), US 337 (11), US 307 (10).
communis x *ussuriensis*	2	3	*ussuriensis:* Hansen's Seedling (2)
communis x *calleryana*	7	8	*calleryana:* Bradford (7)
communis x *ussuriensis-communis*	1	2	*ussuriensis-communis:* Tioma (1) *communis:* US 278 (1)
communis x *pyrifolia-communis*	66	39	*pyrifolia-communis:* Kieffer (14), US 643 (13)
communis x other	9	11	(*pyrifolia* x *ussuriensis*) x *communis:* NJ 4876 1092 (9)
communis x unknown	44	34	*communis:* Moonglow (6) unknown: Richard Peters (9)
calleryana x *pyrifolia-communis*	2	3	*calleryana:* Bradford (2)
calleryana x unknown	1	2	*calleryana:* Bradford (1) unknown: Richard Peters (1)
pyrifolia-communis x *pyrifolia-communis*	11	9	NJ 490871089 (4), NJ 5001480202 (3), NJ 5001710820 (3), NJ 5008710504 (3)
pyrifolia-communis x other	1	2	*pyrifolia-communis:* NJ 490871089 (1) other: NJ 48761092 (1)
pyrifolia-communis x unknown	6	11	unknown: US 56112-146 (2)
other x unknown	2	3	(*pyrifolia* x *ussuriensis*) x NJ 48761092 (2)
unknown x unknown	5	8	US 56112-146 (3)
Totals	256	81	

Table 2. Calculations of adjusted parental fire blight resistance.

Clone	Trial I	II	III	IV	V	Mean	Adjusted mean
Bartlett	2.8	3.0	1.9	1.0	3.0	2.3	
Moonglow	8.5	8.6	7.5	7.0	7.0	7.7	
Magness	9.3	8.8	8.6	7.0	8.0	8.3	
Base mean	6.9	6.8	6.0	5.0	6.0	6.1^z	
Kieffer	4.3	5.8		4.0	6.0		5.0^y
Dawn	7.0	6.5	5.2	6.0			6.2
Old Home	7.8			7.0	7.0		7.5
Waite	9.0						8.0
Richard Peters	8.5			9.0			8.4
Bradford			9.0	9.0			10.1

^{z}Grand mean.

$^y[(\frac{4.3}{6.9} \times 6.1) + (\frac{5.8}{6.8} \times 6.1) + (\frac{4.0}{5.0} \times 6.1) + (\frac{6.0}{6.0} \times 6.1)] \div 4 = 5.0.$

ness', and 'Moonglow') and the grand mean of the elite group are shown in Table 6.

The progeny means of all other crosses (124 in total) involving one or more of the elite parents were then adjusted to the grand mean of the elite set of crosses to give a measure of the relative average combining ability of each parent, on the basis of performance relative to the base mean of the appropriate elite parents. The formula is identical in form to that used to calculate adjusted mean parental phenotypic scores, where,

$\hat{P}_i$ = the estimated average combining ability of the ith parent;
A_{ij} = the mean of the cross between the ith parent and the jth elite parent;
$\bar{B}_j$ = the base mean of the jth elite parent;
$\bar{G}$ = the grand mean of the standard × elite set of crosses;
J_i = that set defining those elite parents involved in crosses with the ith parent;
$n(J_i)$ = the number of crosses to the elite group to the ith parent;
$j \square J$ = j takes those integer values in set J.

An example of the method is given in Table 6.

Results and Discussion

Parental blight phenotypes. Adjusted parental fire blight resistance values and the number of trials upon which the means are based are presented in Table 4. The parents are also identified in respect to species and sensitivity genotype, as proposed by Thompson et al. (20). The range of adjusted values varied from 0.9 for 'Tioma' to 11.0 for US 342 and US 60415-001 ('White Anther').

While small numbers of parents limited the distributions in some species pedigrees, the parents represent a broad range of resistance (Table 5). The sole parents of *P. ussuriensis* Maxim., 'Hansen's Seedling', and of *P. calleryana* Decne., 'Bradford', were rated as highly resistant. The *P. ussuriensis-P. communis* hybrid, 'Tioma', however, was rated as highly susceptible. Two clones, NJ 487601092 and Illinois 48, designated as of "other" pedigrees, were rated as very high (9.4) and moderately low (2.9) in resistance. Both are progeny of Illinois 76 (probably a hybrid of *P. pyrifolia* (Burm.) Nakai and *P. ussuriensis*) × 'Bartlett' (*P. communis*) crosses. The parents of *P. communis, P. pyrifolia-P. communis* hybrids, and unknown pedigrees, however, were distributed across the entire range of values.

The accuracy of the method of estimation depends upon the number of trials upon which an adjusted mean phenotypic value is based, with less confidence being placed in a relative phenotype as the number of trials in which a parent occurred decreases. A total of 38 parents appeared in only one trial, 23 appeared in two trials, 8 in three trials, 3 in four trials, and only the 4 standard parents appeared in all five trials. The adjusted scores must, therefore, be considered to be only approximate. Considerable variability may exist between trials due to environmental effects. An advantage of the method is that the parental phenotypes are not arbitrarily assigned. Examination of the adjusted scores has revealed no gross deviations from reported values or rankings.

Estimation of heritability. Values for heritability (h^2), standard deviation of the heritability (s_{h^2}), correlation coefficient, (r), and the coefficient of determination (R^2), are shown in Table 6. In general, heritability values based upon progeny means indicated moderately high amounts of additive genetic variance within the population studied. Significant heritability within 4 species crosses (*P. communis* × *P. communis, P. communis* × *P. communis-P. pyrifolia* hybrids, *P. communis* × unknown, and *P. communis-P. pyrifolia* × *P. communis–P. pyrifolia*) differed little from each other (h^2 = 0.52 to 0.58), or from the estimate for the entire population (h^2 = 0.52). The similarity of heritabilities within reported species crosses indicates that none of these particular species mating systems is more efficacious for transmitting resistance, confirming data

Table 3. Estimation of average combining ability (see Table 4).

Clone	A Bartlett	Kieffer	Magness	Moonglow	B Bradford	US 307	US 301	US 539	Means A	B	A+B	Adjusted mean
Bartlett		3.8	4.5	4.3	4.2	3.1	5.1	3.4	4.2	3.9	4.0	
Kieffer	3.8		5.7	5.9	5.4	4.5	4.4	5.4	5.1	4.9	5.0	
Magness	4.5	5.7		5.7	6.1	5.5	5.7	3.2	5.3	5.1	5.2	
Moonglow	4.3	5.9	5.7		5.3	5.5	4.9	5.7	5.3	5.3	5.3	
Base mean	4.2	5.1	5.3	5.3	5.2	4.6	5.0	4.4	5.0	4.8	**4.9**^{z}	
Conference*				2.7		3.1	2.9	3.6				3.1^y
Max-Red Bartlett			4.6	4.3			3.6					3.9
Maxine			5.8		5.2		4.4					4.9
US 309		6.6	5.7			7.3		6.3				6.6
US 264		6.8	7.3	8.9				8.4				7.7

^{z}Grand mean.

$^y[(\frac{2.7}{5.3} \times 4.9) + (\frac{3.1}{4.6} \times 4.9) + (\frac{2.9}{5.0} \times 4.9) + (\frac{3.6}{4.4} \times 4.9)] \div 4 = 3.1.$

A = standard parents; A+B = elite parents.

Table 4. Parents, species, sensitivity genotype, adjusted phenotypic scores (APS) and estimated average combining ability (ACA) for fire blight resistance. The number of trials or crosses from which each mean is based is in parenthesis.

Parent	Species[z]	Sensitivity genotype[y]	APS (no. trials)	ACA (no. crosses)
US 60415-001	unk	sese	11.0(1)	–
US 342	com	sese	11.0(1)	8.2(1)
US 56112-114	unk	sese	10.3(2)	–
Bradford	cal	sese	10.1(2)	5.1(4)
Hansen's Seedling	uss	sese	10.0(1)	–
US 264	com	sese	9.8(1)	7.7(4)
US 56111-008	unk	sese	9.7(1)	–
US 278	com	–	9.4 (1)	5.5(2)
NJ 487601092	other	sese	9.4(3)	–
US 337	com	sese	9.0(2)	4.8(3)
Tenn. 34S197	pyr-com	sese	8.6(1)	4.5(2)
US 1832	com	sese	8.6(1)	4.4(2)
US 56109-043	com	–	8.5(1)	–
Richard Peters	unk	–	8.4(2)	5.0(3)
Magness	com	sese	8.3(5)	5.2(7)
Waite	pyr-com	sese	8.0(1)	6.4(2)
US 505	com	sese	7.8(2)	5.3(2)
Moonglow	com	sese	7.7(5)	5.3(7)
US 56112-146	unk	sese	7.6(2)	6.8(1)
US 56112-119	unk	sese	7.6(2)	5.8(2)
Old Home	com	sese	7.5(3)	5.3(3)
NJ 5001480202	pyr-com	sese	7.4(3)	5.1(4)
US 309	com	sese	7.3(1)	6.6(4)
US 414	com	–	7.3(1)	–
US 1753	com	sese	7.1(3)	6.3(1)
US 301	com	sese	7.1(3)	5.3(5)
US 386	com	sese	7.1(1)	6.1(2)
US 643	pyr-com	sese	6.9(2)	5.3(6)
US 539	com	sese	6.8(3)	4.3(4)
US 307	com	sese	6.7(2)	4.8(5)
US 201E	pyr-com	–	6.4(1)	–
Dawn	com	sese	6.2(4)	4.5(4)
US 521	com	sese	6.1(1)	5.1(1)
US 725	com	sese	6.1(1)	–
Mich-US 437 (2x)	com	–	6.1(1)	–
NJ 5001710820	pyr-com	sese	6.1(2)	4.6(2)
US 56112-066	unk	–	5.6(1)	–
US 56127-003	unk	–	5.6(1)	–
Maxine	com	sese	5.3(4)	4.9(3)
Fort Valley	unk	–	5.3(1)	3.4(1)
Kieffer	pyr-com	sese	5.0(4)	5.0(7)
Comice	com	Sese	4.7(3)	3.8(3)
US 446	com	–	4.0(2)	5.0(2)
Mich-US 572 (4x)	com	–	4.0(1)	–
US 56112-075	unk	–	3.4(1)	–
Charles Escaig	unk	–	3.4(2)	2.5(1)
Max-Red Bartlett	com	Sese	3.0(2)	3.9(3)
Illinois 48	other	–	2.9(1)	5.3(1)
US 56121-008	unk	–	2.8(1)	–
Mich-US 504-2	com	–	2.7(1)	–
NJ 501971211	pyr-com	–	2.7(1)	–
Parberton (4x)	com	–	2.6(2)	4.3(1)
Beurre Bosc	com	Sese	2.6(3)	3.8(1)
US 447	com	–	2.4(1)	4.5(1)
NJ 490871089	pyr-com	–	2.4(1)	–
NJ 5008710504	pyr-com	–	2.4(1)	–
Bartlett	com	Sese	2.3(5)	4.0(7)
Turkey 7	unk	–	2.2(2)	3.8(2)
Lincoln	com	–	2.2(1)	4.1(2)
Pioneer	unk	Sese	1.9(2)	3.4(3)
Seckel	com	–	1.9(2)	4.1(2)
NJ 5001480917	pyr-com	–	1.8(3)	–
Roi Carlo de Wurtenberg	com	–	1.8(1)	–
Pulteney	com	–	1.7(2)	5.0(2)
Clyde	com	Sese	1.5(2)	3.5(3)
Thompson's	unk	–	1.5(1)	–
NJ 501971234	pyr-com	Sese	1.5(2)	3.2(3)
Gorham	com	Sese	1.4(2)	4.6(1)
Winter Nelis	com	–	1.3(1)	–
d'Anjou	com	Sese	1.2(1)	4.1(3)
Ewart	com	–	1.2(1)	5.8(2)
US 938	pyr-com	–	1.1(1)	–
Conference	com	Sese	1.1(2)	3.1(4)
Marie Louise	com	Sese	1.1(2)	–
Ananas de Courtrai	com	Sese	1.0(3)	3.2(1)
Tioma	uss-com	–	0.9(1)	–
Miss-US 3-15M	unk	–	–	5.9(1)
Miss-US 3-53M	com	–	–	5.1(2)
Mich-US 437 (4x)	com	–	–	4.6(1)
Minn. 5	unk	–	–	4.3(3)
US 220	com	–	–	4.1(1)
US 562	com	–	–	3.8(1)

(Continued)

[z] Species are abbreviated as follows: com = *P. communis*, cal = *P. calleryana*, uss = *P. ussuriensis*, pyr = *P. pyrifolia*, other = (pyr × uss) × com, unk = unknown.

[y] Sensitivity genotypes, *Sese* and *sese*, are as assigned by Thompson et al. (20).

previously reported by Layne et al. (14). The precision of the heritability estimates was moderately high, with s_{h2} values no higher than ±0.17 and R^2 values ranging from 0.36 to 0.48. The estimates of heritability should, therefore, be reasonably reliable predictors of the average rate of additive genetic gain in progeny means. Additional progenies are needed to draw conclusions about species crosses not reported herein.

When the means of 20 progenies of 'Bartlett' were regressed against their mid-parental values, the heritability value was significantly reduced ($h^2 = 0.27 \pm 0.13$). The regression coefficient was not significantly different from zero, and the R^2 value of 0.19 was substantially lower than those obtained for the subpopulations discussed above. This low value for 'Bartlett' may be explained by the presence of a major dominant gene for susceptibility within *P. communis* postulated by Thompson et al. (20) from an analysis of segregation patterns using these same data. 'Bartlett' as well as various susceptible parents were assigned the heterozygous genotype (*Sese*); resistant parents were assigned the genotype *sese*. None were assigned the genotype *SeSe* (Table 4). These genotypes suggest substantial nonadditive sources of variation.

The effect of the sensitivity gene was examined by estimating and comparing heritabilities within crosses between parents of the various sensitivity genotypes (Table 6). It was expected that the presence of a dominant gene for susceptibility entering a cross would significantly lower heritability of resistance. When comparing crosses involving nonsensitive parents (*sese* × *sese*), a heritability of $h^2 = 0.46 \pm 0.13$ was calculated. However, the correlation coefficient ($r = 0.36$) and the coefficient of determination ($R^2 = 0.13$) were lower than those of the entire population. Crosses between the heterozygotes (*Sese*) and the nonsensitive homozygotes (*sese*) had a significantly (1% level) lower heritability estimate of $h^2 = 0.29 \pm 0.12$. Again, the values of the correlation coefficient ($r = 0.28$) and the coefficient of determination ($R^2 = 0.08$) were lower than the statistics observed in the whole population. The heritability calculated for *Sese* × *Sese* crosses would be expected to be lowest. The observed value was $h^2 = 0.50$, but was not significantly different from zero. Insufficient data was available for a definite analysis of this combination of sensitivy genotypes because only 11 crosses between highly susceptible parents were made.

Progenies within *P. communis* showed unexpectedly high heritability values for *Sese* × *sese* ($h^2 = 0.71 \pm 0.19$) and *sese* × *sese* ($h^2 = 0.80 \pm 0.24$) crosses, and these were significantly higher than the corresponding values for total progenies within *communis*, 0.29 and 0.46, respectively, (significance test not shown). The dominant allele decreased heritability within *P.*

Table 5. Distribution of parental adjusted phenotypic scores (APS) and average combining ability (ACA) for resistance to fire blight, by species in pear.

Pyrus species	Variable	Total no. parents	Distribution by phenotypic score 0.1-1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	5.1-6.0	6.1-7.0	7.1-8.0	8.1-9.0	9.1-10.0	10.1 11.0	Mean	SD
ussuriensis	APS	1										1		10.0	
	ACA	0													
calleryana	APS	1										1		10.0	
	ACA	1						1						5.1	
communis	APS	41	1	9	7	2	1	1	6	8	3	2	1	4.0	2.9
	ACA	37				8	15	9	3	1	1			4.9	1.1
pyrifolia-communis	APS	14		3	3		1		3	2	1	1		5.0	3.0
	ACA	7				1	3	2	1					4.9	1.0
assuriensis-communis	APS	1	1												0.9
	ACA	0													
other	APS	2			1							1		6.2	4.6
	ACA	1						1						5.3	
unknown	APS	16		3	2	2		3		2	2		2	5.3	3.0
	ACA	10			1	4	2	2	1					4.4	1.4
Total	APS	76	2	15	13	4	2	4	9	12	6	6	3	5.1	3.0
	ACA	56			1	13	20	15	5	1	1			4.8	1.1

communis crosses (0.80 vs. 0.71) as expected, but the difference was not significant.

The estimates of heritability within subpopulations defined by parental sensitivity genotypes deviated significantly from the estimates obtained within the larger populations of species crosses and of all progenies combined. Sampling error due to few crosses may account for some of the differences in each case. However, if the dominant allele for susceptibility does exist, and the differences in the heritabilities is confirmed from planned studies of larger populations, estimates of average response to selection must be based upon consideration of appropriate parental sensitivity genotypes. Estimates of heritability obtained from crosses between parents of the sensitivity genotypes represent an average effect and may not apply to all subpopulations.

Our results indicate that additive genetic sources of variation in progeny means exist in sufficient amount to enable a reasonable rate of genetic advance in resistance to fire blight. Additive genetic variance accounts for about 50% of the variance over all crosses. Assuming that variation due to environment is nearly equal in all crosses, the remaining variation is due to nonadditive effects. Analysis of resistance using the sensitivity genotypes assigned by Thompson et al. (20) offer evidence for the existence of nonadditive genetic effects associated with certain parents. However, our test cannot be considered definitive, because it is not an independent evaluation, being based upon the same population.

Parental prepotency. Adjusted mean progeny scores for fire blight resistance were calculated and used as estimates of relative average combining ability for 56 parents (Table 4). The mean scores for average combining ability ranged from 2.5 for 'Charles Escaig' to 8.2 for US 342, with an overall mean of 4.8 ± 1.1. The values were heavily concentrated between 3.1 and 6.0 (Table 5).

The parents for which values could be calculated represent 5 "species" groups (*communis, pyrifolia-communis* hybrids, *calleryana,* other, and unknown). The most numerous, *P. communis,* included 37 parents, whose mean adjusted progeny resistance scores ranged from 3.1 for 'Conference' to the two overall highest parents, US 342 and US 264, rated at 8.2 and 7.7, respectively. These last two parents, as well as 'Magness' transmit their own high levels of resistance to their offspring. The mean value for all *P. communis* parents was 4.9 ± 1.1.

The 7 *pyrifolia- communis* hybrid parents ranged between 3.2 for NJ 501971234 to 6.4 for 'Waite'; the mean adjusted progeny resistance score was 4.9 ± 1.0. Parents of "unknown" pedigree constituted 10 entries, and varied from 2.5 for 'Charles Escaig' to 6.8 for US 56112-146; the average combining ability in this group was 4.4 ± 1.4. 'Bradford' was the only parent of *P. calleryana* origin and was rated 5.1 indicating a failure to transmit its own high degree of resistance. The pedigree "other" was represented by Illinois 48 [(*pyrifolia* × *ussuriensis*) × *communis*], which was rated 5.3.

No species group appeared to be greatly more efficacious than any other for transmitting resistance to fire blight. However, 5 of the 7 parents rated 6.1 or above were *P. communis.*

The reliability of the estimates depends upon the number of parents of the "elite" group to which each parent has been crossed, the size of each progeny, and validity of the assumption of additivity. Most estimates were based upon relatively few progenies. The distribution of elite parent crosses was as follows:

No. of different elite parent crosses	No. of clones
6	1
5	2
4	8
3	10
2	15
1	16

Therefore, the calculated values for an individual parent must be considered in the light of the number and the size of the progenies that make up the mean combining ability estimate.

Analysis of combining ability and heritability studies have a common theoretical basis in the partitioning of variances and may be jointly applied for parent selection. If additive genetic effects predominate over nonadditive genetic effects and the environmental variance is low, heritability will be high and parents may be selected on the basis of their own phenotypes. Tests of combining ability or progeny testing may be applied to identify prepotent parents. If nonadditive effects are significant, however, progeny testing may be needed to identify the best parents and parental combinations. If the parental phenotypes assigned in this study indicate relative average combining ability, then selection of parents on the basis of phenotype could be a preliminary procedure for reducing the number of crosses to be made and the number of seedlings to be evaluated.

Table 6. Heritability estimates of fire blight resistance in pear.

Cross	n	h^2	s_{h^2}	r	R^2
Total progenies^z	227	0.52**	0.04	0.66**	0.43
communis × *communis*	96	0.52**	0.06	0.68**	0.46
communis × *pyrifolia-communis*	56	0.50**	0.09	0.60**	0.36
communis × unknown	32	0.58**	0.12	0.67**	0.45
pyrifolia-communis × *pyrifolia-communis*	13	0.55**	0.17	0.69**	0.48
Bartlett progenies	20	0.27	0.13	0.43	0.19
sese × *sese*					
Total	79	0.46**	0.13	0.36**	0.13
communis × *communis*	33	0.80**	0.24	0.52**	0.27
Sese × *sese*					
Total progenies	76	0.29*	0.12	0.28*	0.08
communis × *communis*	37	0.71**	0.19	0.54**	0.29
Sese × *Sese*					
Total	11	0.50	0.75	0.22	0.05

^{z}Estimates from single-parent regression were $h^2 = 2b = 0.51$.
**,*Significant at 1% (**) or 5% (*) level.

Comparison of rankings of parental phenotypes and the corresponding average adjusted progeny scores indicate some cases of substantial deviations in rank position (Table 4). For example, 'Ewart', Illinois #48, 'Pulteney', 'Gorham', and 'Beurre d'Anjou' appear to be ranked considerably higher for adjusted progeny means relative to their rank based on phenotype, while US 278, 'Bradford', 'Richard Peters', US 337, Tenn. 34S197, US 1832, 'Doyenne du Comice', 'Fort Valley Unknown', and 'Charles Escaig' appear to be ranked lower. Given the approximate nature of the average adjusted progeny means, however, and with the exceptions listed above, the parental phenotypic scores generally agree with their adjusted progeny means, or combining ability scores, within broad groupings of low, moderate, and high combining ability. These groups may be arbitrarily defined by the limits of 2.5 – 4.0, 4.1 – 6.5, and 6.6 – 8.2 for mean progeny resistance scores. Our results agree very closely with those previously reported (14, 15, 23). Although nonadditive effects, including perhaps the postulated dominant allele for susceptibility, are present, additive genetic effects account for approximately one-half of the phenotypic variability in progeny means within the whole population. The nonadditive effects vary among specific parents. Selection and mating procedures, therefore, must be based on the existence of nonadditive as well as additive genetic effects. Selection against those parents that contribute to the susceptibility of their offspring should be practiced to increase the frequency of favorable alleles, and, as suggested by Thompson et al. (20), to decrease the frequency of the dominant allele (*Se*) in the breeding population.

In general, most of the parents assigned the dominant allele have low fire blight resistance scores, and, therefore, may be selected against on the basis of their own phenotypes. Initial screening of seedlings on this basis will eliminate the least prepotent genotypes from those selected for use as parents in a new generation of matings. Some degree of progeny testing with greater numbers of seedlings per cross will also be necessary to identify the most prepotent parents, as suggested by Layne et al. (14) and van der Zwet et al. (23).

The high heritability reported within crosses between nonsensitive (*sese*) *P. communis* parents indicates that selection for resistance within progenies of this subpopulation will result in a high amount of genetic gain.

Control of environmental variation and of the infection process, through greenhouse screening of artificially inoculated seedlings, would decrease the proportion of nongenetic variance contributing to the total phenotypic variance and eliminate complicating genotype-environment confounding. These measures would allow more efficient evaluation of resistance, leading to selection of the more prepotent parents, and more rapid genetic advance for fire blight resistance.

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