

Genetic variability and preliminary heritability estimates of resistance to scab (*Venturia inaequalis*) in an apple genetics population

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Abstract The genetic diversity of scab (*Venturia inaequalis* (Cke.) Wint.) resistance was studied on two of the four sublines of the HortResearch Apple Genetics Population. Subline 91 consisted of 214 families and was evaluated in its 6th leaf, and subline 94 consisted of 75 families and was evaluated in its 3rd leaf at Havelock North. A total of 253 families were derived from open-pollinated seed from apple cultivars (*Malus* × *domestica* Borkh.), as well as crabapples (*Malus* spp.) from various countries, including 52 families derived from seed collected in Kazakhstan. The other 36 families resulted from controlled crosses. Seedlings at two sites (Havelock North and Riwaka) were individually rated on a 10-point scale (from 0 = not infected to 9 = very highly infected) for the amount of scab on the leaves (two sites) and fruit (one site only) after natural infection in orchards where no fungicides were applied in the season of evaluation. The overall average scab score was 1.61 for the open-pollinated families with known provenance in subline 91, with the lowest score for the families from the Netherlands (1.03), followed by Denmark (1.27) and Sweden (1.30). For

subline 94, the average scab score for the Kazak families (2.60) was much lower than that for the families derived from cultivars (3.57). There was a fair relationship between the scab levels on the leaves and the fruit ($R^2=45.8\%$). The estimated heritability of scab resistance was moderate (c. 0.30) for some subsets of the Apple Genetics Population, which is sufficient for the efficient development of new apple cultivars with durable resistance. However, heritabilities were much lower for the full-sib families of subline 91 and the Kazak collection in subline 94. Based on their mean scores, 31 families were identified as having the highest potential for improving scab resistance in apple.

Keywords *Malus*; heritability; resistance breeding

INTRODUCTION

Apple scab, caused by *Venturia inaequalis* (Cke.) Wint., is a major fungal pathogen of apples affecting the productivity of the trees as well as the appearance of the fruit. Prevention and eradication are difficult because of the necessity of careful timing of fungicide applications. An effective, long-term strategy for control of scab is the development of resistant cultivars, thus reducing the reliance on chemical sprays.

In a recent review on the topic, McHardy (1996) describes the development of scab resistant apple cultivars since *Malus floribunda* 821 was identified as a source of resistance (Hough 1944). Currently, most of the resistant commercial apple cultivars carry the major gene V_f that was identified in *M. floribunda* 821 (Crosby et al. 1992). Another 10 independent apple scab resistance loci (V_a , V_b , V_{bj} , V_{ft} , V_g , V_{h2} , V_{h4} , V_{jonsib} , V_m , and V_r) have been named (Laurens & Lespinnas 1996; Bénaouf & Parisi 2000; Bus et al. 2000). However, the identification of virulent races of *V. inaequalis* overcoming several of the resistance genes (McHardy 1996), including the V_f gene (Parisi et al. 1993), is an indication of the risk of resistance breakdown to which apple

cultivars with single resistances are exposed. The risk of resistance breakdown stresses the need to search for alternative sources of genetic resistance, and to develop cultivars with gene combinations resulting in durable resistances.

At the Horticulture and Food Research Institute of New Zealand Ltd (HortResearch), an apple genetics population has been developed to establish and maintain biodiversity for cultivar development (Noiton & Alspach 1996), as well as to study genetic aspects of important traits (Noiton & Shelbourne 1992). This population is anticipated to provide novel sources of monogenic and polygenic resistances to a range of pests and diseases for application in a long-term breeding strategy based on recurrent selection. Hence the value of the Apple Genetics Population is determined by the new genes for resistances as well as for other characters (Oraguzie et al. 2000; Oraguzie et al. 2001) it is providing for incorporation into the HortResearch breeding programme. This paper reports on the evaluation of part of this population for apple scab infection, and the preliminary estimation of the heritability of resistance to this disease.

MATERIALS AND METHODS

Plant material and disease evaluation

The HortResearch Apple Genetics Population is divided over four sublines designated 91–94, where the number denotes the year when the seeds were sown. The population was established in orchards at three HortResearch sites (Havelock North, Riwaka, and Clyde) in years 1993–96. In this study, apple scab evaluations were performed on the sublines 91 and 94 at Havelock North (39°40'S 176°53'E), and subline 91 at Riwaka (41°04'S 173°00'E). The trees at Clyde were not assessed as scab infection was extremely low. Subline 91 consisted of 214 families in their 6th leaf, 183 of which were derived from open-pollinated (OP) seed from a range of apple cultivars (*Malus × domestica* Borkh.), as well as crabapples (*Malus* spp.) from various countries (Noiton & Shelbourne 1992). Thirty-one families resulted from controlled crosses where germplasm received in the form of pollen was crossed onto randomly selected apple cultivars in the HortResearch repository. Subline 94 consisted of 75 families in their 3rd leaf: 52 of which were derived from seed collected from wild populations in four regions of Kazakstan in 1993 (Forsline et al. 1993;

Hokanson et al. 1997), 16 from OP seed of apple cultivars, and five from controlled crosses between apple cultivars. The provenances of the accessions were assigned according to the origin as reported in the literature (e.g., Smith 1971), not according to the country from which the seed was received.

For subline 91, 4768 seedlings representing all 214 families (1–90 (mean c. 22) seedlings/family) were present at Havelock North, and 2388 seedlings representing 172 families (4–58 (mean c. 14) seedlings /family) were present at Riwaka. Subline 94 at Havelock North had 1828 seedlings in 72 families (1–100 (mean c. 25) seedlings/family). The trees were planted at a distance of 3×0.75 m as single-tree plots in randomised incomplete blocks of 20 trees allocated using the "Designer" software (K. Russell, University of Wollongong, NSW, Australia pers. comm.). Although usually less of an issue with diseases than pests, natural infections can often be unevenly distributed, which can create problems in data interpretation. Nevertheless, Alspach & Bus (1999) showed that the small block size of 20 trees was adequate to manage the observed patchiness of woolly apple aphid infestation in the Apple Genetics Population.

The seedlings were maintained under a low insecticide and fungicide program, which was ceased from the second half of the growing season (i.e., from January). To enhance natural infection, no fungicides or insecticides were applied during the 1997/98 growing season when the scab assessment was done. Subline 91 was evaluated over the period 2–23 December 1997 at Havelock North and 18–24 December 1997 at Riwaka, and subline 94 over the period 12–15 January 1998.

In a preliminary evaluation of c. 100 trees, a method consisting of counting scab lesions in a 10-s period on the leaves of a randomly selected branch of similar size from each tree was trialled. As this method was too laborious, we decided to develop a 10-point scale from these data to estimate the density of the scab lesions on the leaves from 0 (no infection) to 9 (multiple lesions on most leaves). At Havelock North, leaf assessments were performed by two people: the first five rows of subline 91 by one, and the remaining 12 rows and subline 94 by another. At Riwaka, the assessments were carried out by a third person, using the same scale for the leaf assessments. The latter also separately estimated the proportion of the fruit infested (multiplied by 10). Other fruit data were collected separately as part of the wider objective of the genetics programme (Oraguzie et al. 2000).

Statistical analyses

Mixed effects models were fitted to the data:

$$y_{ijkl} = \mu + S_i + S_i / B_j + P_k + P_k / F_l + S_i \times (P_k / F_l) + \epsilon_{ijkl} \quad (1)$$

where y_{ijkl} was the leaf or fruit scab score for the tree from the l^{th} family F of the k^{th} provenance P planted in the j^{th} incomplete block B within the i^{th} evaluation site S . Sites, provenances, and families were modelled as fixed effects; blocks were taken as random. The model was fitted to each subline independently and, within each subline, the full-sib (FS) and OP families were treated separately. For subline 91, data from each site were fitted separately and together. Where applicable, a reduced model was fitted (e.g., subline 94 had no site component).

Family means, computed from the restricted maximum likelihood (REML) analyses, were subject to one-way analyses of variance to examine provenance differences. In addition, mean scores were ranked, and the confidence intervals for each rank determined by bootstrapping the residuals. The residuals from the REML analysis were re-sampled with replacement and added to the means to give a new data set of the same size as the original. Simple family means were then computed from this new data set, and ranked. The difference between the new rank and the original rank was calculated. The procedure was repeated 100 times. The lower bound was determined by taking the mean of those ranks lower than the original and half the exact matches; and the upper bound by averaging those ranks higher than the original and half the exact matches. This is a modification of the method suggested by Andersson et al. (1998).

We tabulate the means of the better families only, i.e., those which ranked in the top 15% for both the upper and lower bound.

Estimation of heritabilities

Preliminary heritabilities were estimated to assess the potential value of this germplasm in scab resistance breeding before further investments were made into the programme by commencing the intended recurrent selection process (Noiton & Shelbourne 1992). Heritabilities were computed from the variance components, estimated from Equation 1 using REML analyses with families as a random effect, as:

$$h^2 = \frac{k \times \sigma_f^2}{\sigma_{total}^2} \quad (2)$$

where σ_f^2 is the variance among families within regions, σ_{total}^2 is the total phenotypic variance, and

k is the coefficient of relationship (Falconer & Mackay 1996). With n pollen parents per family:

$$k = \left(0.25 + \frac{0.25}{n} \right)^{-1}$$

which is 2 when $n = 1$ (FS) and tends to 4 as n tends to infinity. We have calculated the heritabilities for the whole interval of k , as well as for $k = 2.67$, which equates to $n = 2.1$. At this value for k , the heritability is either overestimated at a maximum of 33% if actual $n = 1$, or underestimated at a maximum of 33% if actual $n = \infty$. Standard error estimates of the heritabilities were derived from Dickerson’s method for obtaining estimates of the variance of a ratio as suggested by Dieters et al. (1995).

The number of trees per family varied considerably, from 1 to 100. To check that low replication was not unduly influencing the heritability estimates, some of them were computed after excluding families with four or less trees.

REML-based estimators are robust to violations of the normality assumption (Dieters et al. 1995). However, this robustness does not necessarily apply to the estimates of the standard errors of the estimates. Thus, for sets of data where the residual plot indicated a severe deviation from the normal distribution, jackknife estimates of the standard errors were derived. The jackknife estimator for the standard error of the heritability estimate h^2 is

$$\hat{\sigma}_{JK} / \sqrt{N}, \text{ where:}$$

$$\hat{\sigma}_{JK}^2 = (N - 1) \sum_{i=1}^N (h_i^2 - h_{..N}^2)^2;$$

N is the number of families;

$$h_{..N}^2 = \sum_{i=1}^N h_i^2 / N; \text{ and}$$

h_i^2 is the estimator of h^2 computed with the i^{th} group removed (e.g., Buzas 1997).

All statistical analyses were undertaken using S-PLUS Ver 3.3 (Statistical Sciences 1995).

RESULTS

Mean scab scores

For subline 91, mean scab scores (excluding families with less than four trees) ranged from 0.00 to 4.29 for the OP families; and 0.01 to 2.75 for the FS families of subline 91. Pearson’s correlation coefficient between the family means at the two sites was 0.59 (145 degrees of freedom (d.f.)) for the OP families, but only 0.24 (17 d.f.) for the FS families.

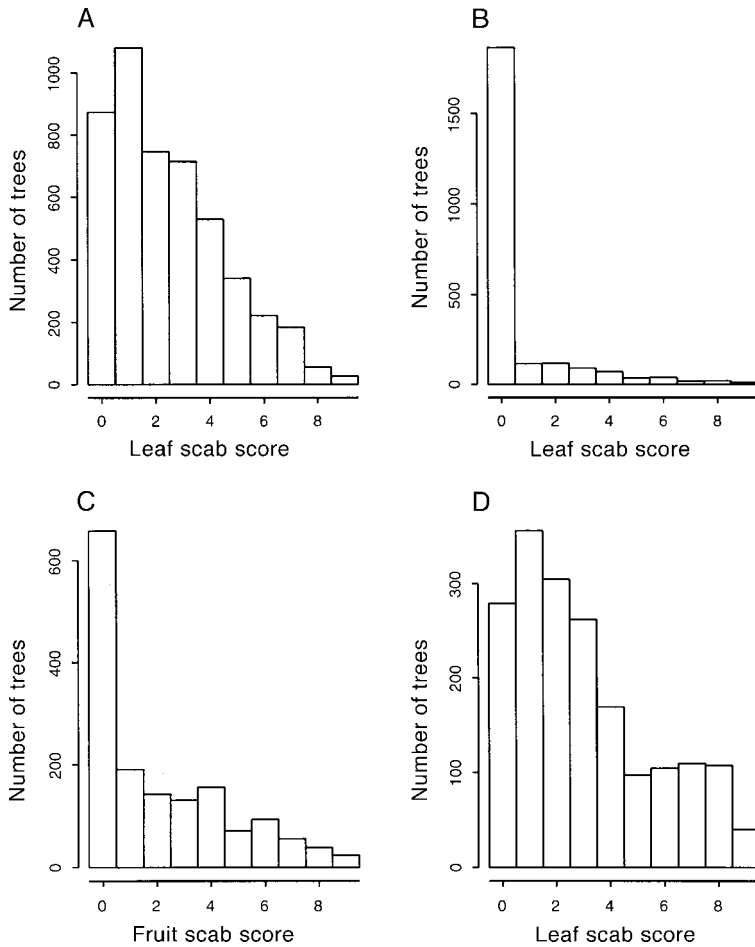


Fig. 1 Frequency distributions of the number of trees in each scab score category: **A**, subline 91 at Havelock North (leaves); **B**, subline 91 at Riwaka (leaves); **C**, subline 91 at Riwaka (fruit); and **D**, subline 94 at Havelock North (leaves).

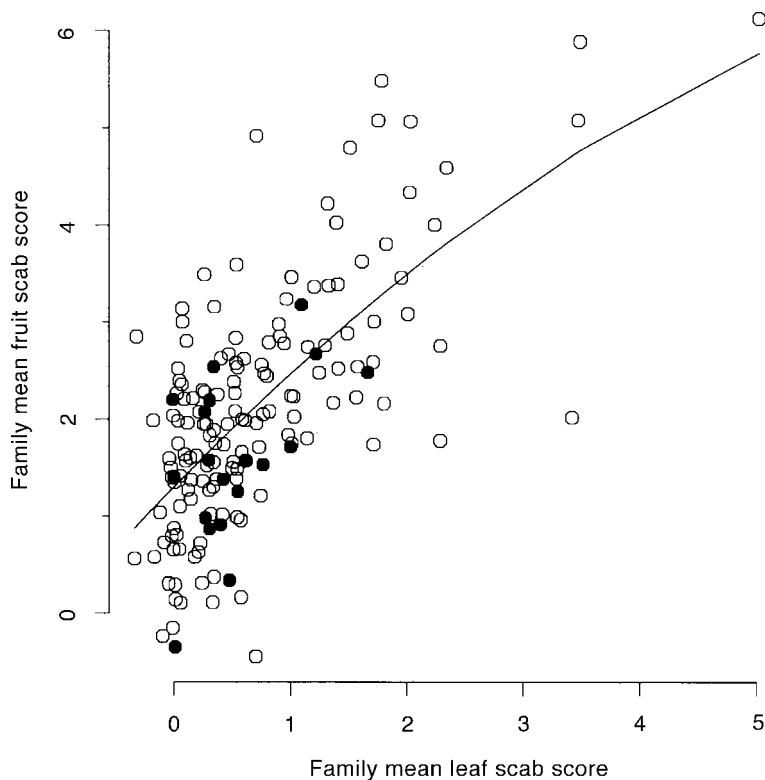
Table 1 Numbers of open-pollinated families, and average family mean scab score and standard error (SE) calculated from the leaf infection data from both sites for the various accessions with known provenances represented in subline 91.

Provenance	No. of families	Mean scab score	SE
Netherlands	26	1.03	0.158
Denmark	15	1.27	0.207
Sweden	9	1.30	0.268
Czechoslovakia	5	1.45	0.359
France	37	1.53	0.132
<i>Malus</i> species	9	1.86	0.268
USSR	22	1.91	0.171
Poland	3	1.93	0.464
United States	26	2.10	0.158
Germany	3	2.23	0.464
Canada	4	2.27	0.402
General mean		1.61	

In this subline, 22 of the 214 families were either known to be crabapples or could be classified as crab type on the basis of fruit size. The mean scab score for all the crabapple families was not significantly different from that for all the other families (1.76 versus 1.99 respectively; $t = 1.14$, $P = 0.258$). The mean scab score differed among provenances in subline 91 ($F_{10,148} = 3.65$, $P < 0.001$) (Table 1). Of the 159 families with known provenance, the 26 families originating from the Netherlands had the lowest mean score at 1.03, followed by the two Scandinavian provenances represented. The small number of families from Canada and Germany had relatively high mean scab scores. That for the *Malus* species was near the general mean.

For subline 94, the mean scab score (excluding families with less than four trees) ranged from 1.26 to 5.00 for the OP families; and from 2.29 to 5.11 for the FS families. There was no detectable

Fig. 2 Relationship between the family mean scab scores for the leaves and fruit from subline 91 at Riwaka, New Zealand. (○, open-pollinated families; ●, full-sib families.) Line shows the quadratic OLS fit ($y = 1.29 + 1.23x - 0.068x^2$; $R^2 = 45.8\%$, residual standard error = 0.90).



difference among the four regions of Kazakhstan ($F_{4,46} = 0.55$, $P = 0.702$), and the among-region variance obtained by fitting regions as a random effect was negligible. The mean score for these regions was 2.60, very close to that for the *Malus* species in the Havelock North population of subline 91. The mean score for the OP families of subline 94 derived from apple cultivars was 3.57, much higher than that for the Kazakhstan families (t value, modified for unequal variances, = 3.45; $P = 0.003$).

The fruit scab score was much higher than that for leaves (subline 91, Riwaka: 2.1 versus 0.7) (Fig. 1B,C). There was a relationship between leaves and fruit for the family mean scab score, although the fruit score was more discriminatory at low levels (Fig. 2). Over 80% of the families had a mean fruit scab score within 1 of that predicted from the mean leaf scab rating.

Over both sublimes, 31 families (c. 10% in each of the sublimes) met the criteria described in the previous section based on their mean scores (Table 2).

Heritability estimates

The level of scab on the apple leaves was similar for the two sublimes at Havelock North (Fig. 1A,D). However, the level at Riwaka, where 78% of the trees had no scab, was much lower (mean = 0.7; Fig. 1A,B).

The heritability estimates derived after excluding families with less than four trees were very similar to those obtained when all families were used (data not shown). Thus, unless otherwise mentioned, the quoted heritabilities were estimated using all relevant families.

For subline 91, four families were excluded from the analysis, as they were the only representatives of their provenance. Other provenances were represented by between three and 37 families.

Heritabilities based on the leaf infection data of the half-sib OP families were up to 0.32 for $k = 2.67$, and up to 0.48 when k tends to infinity (Table 3). However, those for FS families of subline 91 were considerably lower, and did not differ significantly

Table 2 Number of trees (*n*), mean family scab scores, and rank for families in the top 15% of both the lower and upper bound of the rank based on the leaf infections. Refer to the text for details of the computation of the bounds.

Female parent	Male parent	<i>n</i>	Mean	Rank	Lower bound	Upper bound
Subline 91						
Open-pollinated families						
Grote Zoete		5	0.00	1	1	15
White Angel		35	0.11	2	2	8
Cusset		4	0.27	3	2	28
Schneeappel		6	0.30	4	2	25
Russian apple 12740-7A		12	0.30	5	3	19
<i>Malus sylvestris</i>		15	0.40	6	4	22
Pigeonnet Rouge		17	0.41	7	4	23
<i>Malus floribunda</i>		41	0.44	8	6	22
Lunterse Present		9	0.45	9	5	31
Maglemer		46	0.46	10	7	20
Rode Tulpappel		10	0.49	12	6	39
<i>Malus × atrosanguinea</i>		42	0.52	13	9	24
Hans Trio		11	0.53	14	7	41
Geelzoet		71	0.55	15	11	24
Schöner von Wiltshire		8	0.56	16	7	51
Racine		19	0.56	17	11	37
Lunterse Pippeling		16	0.57	18	10	42
Zure Kroon		71	0.62	19	15	30
Tayeshnoe		36	0.64	20	14	36
Full-sib families						
Bisquet Cider	Judor	1	0.00	1	1	7
Fuero Rous	Jeanne Renard	11	0.01	2	2	4
Gloire de Ponchartrain	Bruyère	46	0.47	4	3	6
Subline 94						
Open-pollinated families						
GMAL3560		4	0.91	1	1	10
GMAL3546		7	1.26	4	3	15
GMAL3527		25	1.45	5	4	12
GMAL3530		27	1.62	6	4	14
08-02 <i>baccata</i>		24	1.64	7	5	15
GMAL3566		7	1.64	8	5	24
GMAL3550		12	1.65	9	6	18
GMAL3537		11	1.82	13	7	23
Full-sib families						
Joybells	Beacon	80	2.29	1	1	1

from zero. The fruit infection heritability estimate of the OP families of subline 91 at Riwaka was somewhat lower than that for leaves (Table 3), but were not significantly different. The fruit heritability estimate was negligible for the FS families. The heritability estimate was low (0.12) for the Kazak group within subline 94. However, the heritability estimate for all OP families was similar to those computed for the OP families of subline 91 (Table 3).

The distribution of the residuals of the Riwaka data of subline 91 and the Kazakstan collection of subline 94 both indicated non-normality. The former reflected the high proportion of non-infected trees, and the latter exhibited a skewed distribution. Jackknife standard error estimates were larger (Table 3), and, for the Kazakstan collection, more in line with the other data sets.

For subline 91, when data from both sites were used, the among family variance could be compared

Table 3 Estimates of the heritabilities of apple scab resistance and their Dickerson's and jackknife standard errors, as computed for various subsets of the leaf and fruit (Riwaka, New Zealand, only) infection data. For the open-pollinated families, the estimates for both the range of k (2–4) and $k = 2.67$ are presented.

Families	Site	Heritability		Standard errors	
		Range		Dickerson	Jackknife
Subline 91					
Open-pollinated	Riwaka				
	Leaves	0.23–0.45	0.30	0.045	0.104
	Fruit	0.15–0.29	0.20	0.046	0.083
	Havelock North	0.23–0.47	0.31	0.024	
	Both	0.22–0.44	0.29	0.053	
Full-sib	Riwaka				
	Leaves		0.07	0.046	0.146
	Fruit		0.06	0.052	0.120
	Havelock North		0.11	0.065	
	Both		0.12	0.097	
Subline 94					
Open-pollinated	Havelock North	0.24–0.48	0.32	0.048	
Kazakstan	Havelock North	0.09–0.17	0.12	0.004	0.074
Full-sib	Havelock North		0.37	0.281	

with the site by family interaction variance. For the OP families, the former was an order of magnitude larger than the latter (0.384 versus 0.046). When the FS families were considered, the among-family variance was still larger, but the magnitude of the difference was much smaller (0.108 versus 0.063).

DISCUSSION

Disease evaluation

We were examining germplasm for field resistance to scab, and relied entirely upon natural infection. Scab is widespread within the two apple-growing regions of New Zealand that we considered. However, the levels of infection in Riwaka were low because of the unusually dry 1997/98 growing season (Fig. 1). This necessitated more computer intensive methods for computing the standard errors of the estimates, and probably higher standard errors as well. Nevertheless, the actual heritability estimates were consistent across both sites, suggesting that even at low infections rates the estimate of heritability was robust. Although infection levels at Riwaka were low, the mean infection scores for the OP families within each site were well correlated between the sites (Pearson's correlation coefficient: 0.59). In light of these

findings, it is questionable whether repeated field observations over several years would have improved our estimates. An alternative would have been the use of glasshouse screening. However, no reliable technique was in place at the time of establishment of the Apple Genetics Population. Also, the use of this method on its own has its limitations (Lamb & Hamilton 1969; Kellerhals et al. 1993; Heaton et al. 1995; King et al. 1998).

We found no difference among the four different regions of Kazakstan and negligible variance among regions for mean infection severity. This finding is broadly consistent with that of Lamboy et al. (1996), who found 85% of the enzyme variability present in their Kazakstan populations was attributable to among family within region differences. They concluded that the diversity could be effectively captured by sampling a few large populations. Our results support this conclusion with respect to scab resistance/susceptibility.

Our study confirms the correlation between fruit and leaf infections (Lateur & Populer 1994, 1996; Schmidt 2000). However, whereas scab infection ratings for fruit were consistently higher than those for leaves in our study (Fig. 2), under the European conditions the reverse generally was true, except for some accessions of the russetting type (Lateur & Populer 1994).

Heritability estimates

An incorrect value for the coefficient of relationship k would lead to a bias in the heritability estimate. Because the number of pollen parents is unknown, there is uncertainty in the heritability estimates additional to that estimated by the standard errors. However, by choosing $k = 2.67$, we have reduced the error in the estimates to a maximum of $\pm 33\%$.

The large discrepancy between the OP and FS heritability estimates apparent in subline 91 cannot be attributed simply to an inappropriate choice of k as the FS heritabilities were outside the range for those of the OP families (Table 3). It would appear that the 91 FS families represent a population which is substantially different from the population represented by the OP families of that subline, at least with regard to heritability of scab resistance.

The heritability estimate derived from only the Kazakstan collection of subline 94 was relatively low. The difference in heritability estimates is essentially attributable to differences in the among-family variance, since the residual variance will be about the same. Thus, the increased estimate obtained by including the 16 OP families from apple cultivars, suggests that such families contribute extra heritable diversity. However, this diversity was in the direction of greater susceptibility to scab.

Heritability and resistance breeding

Although there are many reports on the evaluation of apple germplasm for its resistance to scab, including extensive evaluation of old varieties (e.g., Lateur & Populer 1996), reports of genetic studies on this character concerning other than major genes have been few and often involved a limited number of accessions (e.g., Hough 1944; Blazek & Vondráček 1977; White & Bus 1999). In our large-scale study, we found the estimated heritability of scab resistance to be c. 0.3 at $k = 2.67$, which is moderate, but sufficient for the efficient development of new apple cultivars with durable resistance. We included both crab types and *M. domestica* in our heritability estimates since our breeding program involves such inter-specific crosses; i.e., our reference population contains the high level of genetic diversity required for effective recurrent selection (Fehr 1987). Hence, these estimates may be inappropriate for a breeding program restricted to using only *M. domestica*. This is exemplified by the low heritability of the FS families in subline 91 (Table 3) involving only *M. domestica* parents, where limited diversity would restrict potential progress in scab resistance breeding.

Some of the germplasm evaluated in this study contained major genes, which would have inflated the heritability estimates. Three of the families with the lowest mean scores (Russian apple 12740-7A, *M. floribunda* and *M. × atrosanguinea*) are known to carry major gene resistances to apple scab (Laurens & Lespinasse 1996). Since most of the Kazak accessions from which seed were collected were actually (heavily) infected with scab (Forsline et al. 1993) although they were not in our evaluations, it is most likely that major genes are involved here, too. The ubiquitous presence in the Kazak germplasm of genes causing mainly stellate type reactions was confirmed in greenhouse evaluations of seedlings grown from seed collected at the 1995 and 1996 expeditions into Kazakstan (Luby et al. 2001). Some obvious major gene resistances were confirmed in testcrosses and are being introgressed into the eating apple by taking a modified back-crossing approach.

The variance among families was much larger than the site by family interaction variance (by an order of magnitude for the OP families). Shelbourne (1972) has suggested that if the latter variance is less than half of the former, the interaction effect is not of practical importance. This was certainly the case for the OP families, and for the FS the interaction variance was only a little over half that among families. Thus, selection for scab resistance at one site should be sufficient, unless significantly different strains of scab were present at the different sites, which would necessitate the selection across a range of sites. This may not be the case in New Zealand, where the fingerprinting of *V. inaequalis* isolates showed relatively little genetic variation from region to region (E. Rikkerink pers. comm.).

Another issue with the scab fungus is that selection for resistance in the Apple Genetics Population may be complicated as some of the newly introduced accessions may prove to carry resistances that are merely ephemeral because no selection has occurred for the associated virulences in the New Zealand *V. inaequalis* population (MacHardy et al. 2001). However, gene pyramiding is expected to enhance the durability of resistances in apple (Gessler & Blaise 1994; Laurens & Lespinasse 1996). This strategy has been shown effective in, for example, breeding for blast (Correa-Victoria & Martinez 1995) and blight (Huang et al. 1997) resistance in rice, and blackmold resistance in tomato (Robert et al. 2001).

The Apple Genetics Population forms the basis of a recurrent selection program (Noiton &

Shelbourne 1992) in which scab resistance is one of the selection criteria. Individuals have been selected from the families from most sublimes to develop new families for the second phase of genetic studies and population improvement (Oraguzie et al. 2000; Oraguzie et al. 2001). The intention is to develop a selection index to improve the genetic gain and breeding efficiency based on heritability estimates and genetic correlations supported by genetic marker studies.

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