Theor Appl Genet (1998) 96: 1077–1085

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Utilization of pedigree information to estimate genetic parameters from large unbalanced data sets in apple

Received: 14 June 1997 / Accepted: 4 December 1997

Abstract Genetic parameters (narrow-sense heritabilities and genetic correlations) were estimated for major agronomical traits in apple from large unbalanced data sets, with the help of wide-pedigree information. The software REML VCE (Groeneveld 1996) took into account the complex pedigree of the French apple-breeding population, thanks to the restricted maximum likelihood procedure combined with the construction of the entire relationship matrix between hybrids planted in the field and their ancestors. Narrow-sense heritability estimates ranged from 0.34 to 0.68 for traits exhibiting a normal distribution. Heritability values around 0.35–0.40 were obtained for fruit characteristics (size, texture, flavour, juice content, attractiveness, russeting). Higher values of heritability were obtained for vigour, assessed by the circumference of the trunk (0.51), and powdery mildew resistance (0.68). Additive genetic correlations between traits were also estimated, showing a very high relationship between fruit-quality traits. Vigour and powdery mildew resistance were slightly correlated with the other traits. Utilization of the 'individual genetic model' for the estimation of genetic parameters and breeding values in apple is discussed.

Key words Heritability · Genetic correlation · Apple breeding · Pedigree information · Restricted maximum likelihood

Communicated by H. C. Becker

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Introduction

Genetic parameters are useful for selection purposes both for animal and plant breeding. Heritabilities and genetic correlations between traits allow the computation of selection indices and the prediction of genetic gains (Falconer 1981). In plants, mating designs are generally built in order to assess additive and dominant effects: nested, factorial or diallel designs have been predominantly employed. Experimental designs are developed to separate environmental effects (such as block effects) from genetic effects; numerous softwares have been developed to analyse the data from such trials.

Apple breeding is largely developed all around the world. Large breeding programmes were initiated more than 50 years ago in Europe and North America. Common breeding aims are mainly high fruit quality combined with disease and pest resistance (Laurens 1998). In most cases a simple mass selection is applied; more complex selection indices involving breeding values are still poorly developed. Numerous genetic studies have been devoted to the analysis of major genes clearly segregating in progenies (reviewed by Brown 1992). Conversely, very few quantitative genetic studies have been conducted in apple because the work to-date has been mainly devoted to field selection within progenies, rather than analysing well-constructed mating designs. Partial diallel mating designs have been studied in Germany (Dathe 1978, 1979, 1980, 1984, 1985) and France (unpublished). But such designs could not involve many parents, and it was difficult to generalize the results to entire breeding populations. The pedigrees of new apple cultivars are characterized by high levels of relationships among them (Noiton and Shelbourne 1992; Noiton and Alspach 1996). Apple breeders often use the same famous varieties, such as Golden Delicious, Red Delicious, Jonathan or McIntosh in crosses, in combination with new hybrids.

In such a genetic context, the estimation of genetic parameters with traditional mating designs (i.e. factorial, diallel) is biased because of the relationships among the parents involved. This bias is all the more important as several common ancestors are present in the pedigree of the parents in different generations. This is the case for the French apple-breeding population, and probably for all apple-breeding programmes over the world. Conversely, taking into account all the complex relationships among the genotypes makes it possible to estimate more accurate genetic parameters.

In animal breeding, much effort has been devoted to develop well-adapted methodologies to estimate genetic parameters in complex pedigrees (e.g. cattle or pig breeding). Inbreeding is frequently observed when analysing several breeding generations in small populations (in chicken or duck breeding, for example). The 'individual animal model' has been developed to accurately take into account all the pedigree information in a single model describing the whole population (Quaas and Pollak 1980). It allows accurate values of the variance-covariance components to be estimated. Then, the best linear unbiased predictors (BLUP; Henderson 1975) for the genetic evaluation of all genotypes can be computed. Recently, a software package has been developed by Groeneveld (1991, 1996) to compute such estimations for a large range of statistical models in animal breeding (e.g. Ducos et al. 1993; Tixier-Boichard et al. 1995): REML VCE uses a multiple-trait restricted maximum likelihood method for (co)variance component estimations. In the present study, the objective was to apply the 'individual genetic model' methodology to estimate genetic parameters in the French apple-breeding population. This population was initially not constructed for such a purpose, but the characteristics of the individual model, taking into account all the known relationships among individual genotypes, and the availability of the REML VCE software (Groeneveld 1996), allows one to estimate the genetic parameters using a very large apple population. Narrow-sense heritabilities and additive genetic correlations were therefore computed for several agronomical traits scored on more than 12 000 genotypes belonging to more than 200 full-sib families. The results are discussed with regard to basic hypotheses of the individual model and particular features of the data. To our knowledge, our report is the first study concerned with an estimation of the genetic parameters with an 'individual model' methodology within a whole breeding population in plants.

Materials and methods

Breeding population, families and pedigree

The present study focused on a scab-resistant breeding population. The French apple-breeding programme aims at creating new cultivars carrying disease resistances in combination with high fruit quality (Lespinasse et al. 1979; Lespinasse 1989, 1992; Laurens 1994). The two main apple fungal diseases are scab [caused by *Venturia inaequalis* (Cooke) Wint.] and powdery mildew [caused by *Podosphaera leucotricha* (Ell. et Ev.) Salm.]. Regarding scab resistance, numerous crosses have been made for more than 50 years (Crosby et al. 1992) always using the same resistance source derived from a wild *Malus* species (i.e. *Malus floribunda* clone #821). A major gene (*Vf*; Williams et al. 1966) was inherited after the initial cross between clone #821 and a commercial cultivar (Rome Beauty), and has been introduced into the cultivated apple through successive pseudo-backcrosses (Hough et al. 1953; Lespinasse et al. 1979; Crosby et al. 1992). The French scab resistance breeding population consists of crosses between resistant genotypes belonging to the fourth or fifth generation (or more), after the initial cross, and susceptible genotypes (often commercial cultivars, or their offspring). Other crosses involving different resistance sources have also been performed to diversify the genetic sources but are not considered in this study. Because of the frequent exchange of genetic material between France and other countries working on apple breeding for scab resistance, these crosses involved a large sample of the potential genetic variability of the cultivated apple all over the world.

Two hundred and thirteen families were analysed taking into account all the known relationships among them. Two hundred and ten of these had been obtained by controlled crosses performed between 1974 and 1988; the remaining three families were open-pollinated. The pedigree of each parent involved was identified in the research station archives and/or in specific publications of colleagues from other countries. As far as possible, pedigrees employed the oldest cultivars with an unknown parentage (e.g. Fig. 1). The family sizes were unbalanced varying from 2 to 238; the mean family size was 61.9 and about 90% of the families had more than ten individuals. The initial number of genotypes planted in experimental plots was 13 185. Because of mortality and the elimination of trees with very poor or aberrant growth, a maximum of 12 900 genotypes were analysed.

After controlled crosses, seeds were sown and seedlings were first evaluated for scab resistance in the greenhouse (Lespinasse 1992). A mixture of *V. inaequalis* inocula collected in surrounding plots was employed. An early selection was made thereafter based on the resistance symptoms and a variable number of seedlings were selected per family (average selection rate: 40%). These seedlings were then established in the nursery for powdery mildew selection. Here again, a variable number of young trees were selected after two growing seasons (average selection rate: 30%). Then, the selected plants were established in experimental field plots where the data were collected.

Experimental plots and measured traits

The 213 families were evaluated in eight main plots, often subdivided into two or three sub-plots. The 16 sub-plots were planted between 1978 and 1990 with variable numbers of families (Table 1). All plots were located in the same small area (propriety of INRA Angers) except for one located 3 km away (plot 'TN'). Very few families were planted simultaneously in several plots, despite the fact that such families could have been considered as 'bridges' (i.e. connections) between plots. No standard cultivars were involved.

For selection purposes, numerous agronomical traits were measured or scored on each tree planted in the plots. In the present study, only a subset of these traits are analysed: they correspond to the most important ones for apple-breeding purposes (Table 2).

Software utilization and genetic models

Basic statistical analyses were performed with the software S + (Chambers and Hastie 1992). The software REML VCE

Fig. 1 Pedigree of family #205. (o.p.): open-pollination = father unknown

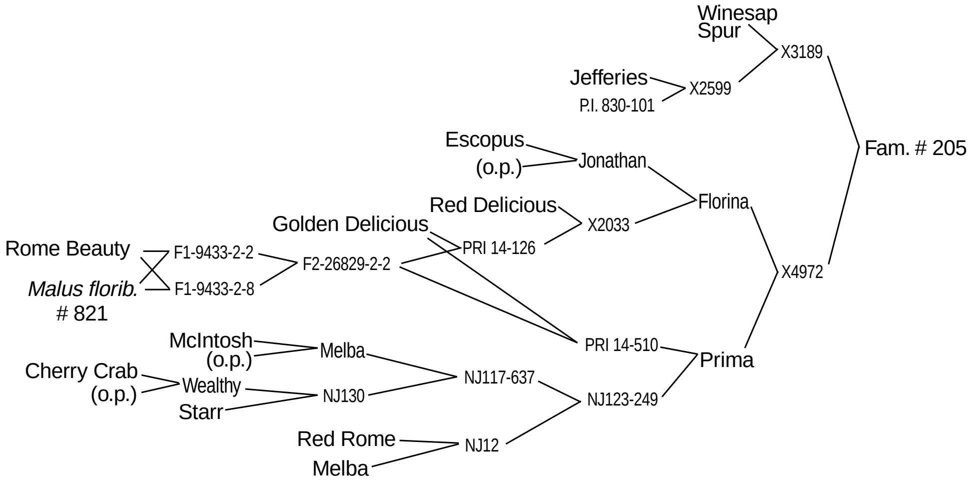

Table 1 Description of the experimental plots. Family #146 is present in both K-B and K-C; family #201 is present in both P42-B and P35-A; family #205 is present in both P35-A and P35-B

Plot	Date of plantation	Number of families	Total number of trees	Spacing[a]
P6 - A	April 1978	20	1276	(4 m + 2.5 m) × 1.4 m
P6 - B	Dec. 1980	15	1042	(4 m + 2.5 m) × 1.4 m
P22 - A	Dec. 1980	16	761	(4 m + 2.5 m) × 1.8 m
P22 - B	Febr. 1983	6	677	(4 m + 2.5 m) × 1.8 m
TN	April 1982	13	1046	(4 m + 2.5 m) × 1.5 m
P15 - A	March 1984	15	987	(4 m + 2.5 m) × 2 m
P15 - B	March 1985	3	204	(4 m + 2.5 m) × 2 m
K - A	March 1985	9	524	(4m + 2.5 m) × 1.8m
K - B	April 1986	31	897	(4m + 2.5 m) × 1.8m
K - C	Febr. 1987	31	1469	(4m + 2.5 m) × 1.8m
P42 - A	March 1988	17	1416	(4 m + 2.5 m) × 1.8 m
P42 - B	Janu. 1989	8	577	(4 m + 2.5 m) × 1.8 m
P35 - A	Janu. 1989	8	489	4 m × 1.6 m
P35 - B	Janu. 1990	15	1121	4 m × 1.6 m
P43 - A	Dec. 1990	9	699	4 m × 1.6 m

[a] (4 m + 2.5 m) × 1.4 m: trees were 4 m or 2.5 m apart (alternately) between rows, and 1.4 m apart within the row

Table 2 Description of the traits with the abbreviations used. The number of classes involved in the trait assessment is given, except for CIR (continuous assessment). The traits were clustered in two groups: normal distribution (N) or L-shape distribution (L)

Abbreviation	Trait description	Number of classes	Group
SIZ	Fruit size	3	N
ATT	Fruit attractiveness	9	N
TEX	Texture of the fruit flesh	5	N
FLA	Flavour of the fruit flesh	7	N
JUI	Juice content of the fruit flesh	5	N
RUS	Russeting of the fruit skin	4	N
CIR	Circumference of the basal part of the trunk	Continuous	N
POW	Powdery mildew resistance in field under natural inoculation	9	N
CRA	Fruit cracking	4	L
WAX	Waxiness of the fruit skin	4	L
BUR	Burrknots on the trunk	4	L

(Groeneveld 1996) was used to compute the genetic parameters. With the restricted maximum-likelihood method (Patterson and Thompson 1971), REML VCE accounts for selection in the data, provided that all information used in selection is included in the analysis. Inbreeding effects are also accounted for in the relationship matrix (Quaas 1976). The software gives both the variance component estimation and the genetic evaluation of all genotypes. Basic model assumptions are: (1) the founders (i.e. highest ancestors) are unselected, unrelated, non-inbred and randomly mated, (2) genetic effects are considered under an infinitesimal model. For practical utilization of REML VCE, two input files were required: the data file, which contained both the effects to be handled in the model and the traits to be analysed; and the pedigree file, which contained all the pedigree information up to the oldest unknown ancestors.

In this study, the statistical model combined a fixed effect (sub-plots) and the individual additive genetic effect (individual-tree genotype effect) specified as a random effect with the relationship matrix included. The model was the same for each trait and had the following structure, in matrix notation:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{e},$$

where $\boldsymbol{y}$ is the vector of observations, $\boldsymbol{b}$ is the vector of sub-plot fixed effects, $\boldsymbol{a}$ is the vector of individual additive genetic values, $\boldsymbol{e}$ is the vector of residuals, and $\boldsymbol{X}$ and $\boldsymbol{Z}$ are incidence matrices relating observations to the effects in the model. Location and dispersion parameters for the random effects were as follows:

$$E\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \quad Var\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

where:

$R = \bigoplus_{j=1}^{m} R_{0ij}$ with m = the number of records, and i = the pattern of missing values for the jth record,

$G = A \otimes G_0$,

R_{0ij} = residual variance-covariance matrix for individual j with pattern i of missing values,
A = numerator relationship matrix,
G_0 = variance-covariance matrix for the additive genetic effect,
$\oplus$ = direct sum,
$\otimes$ = Kronecker product.

The software computed estimates of the additive genetic parameters, i.e. the narrow-sense heritabilities and the additive genetic correlations. Indeed, when the individual genetic effect is specified as a random effect for which relationships exist among the genotypes, the maximum-likelihood estimations of (co)variance components attached to this effect correspond to the traditional additive (co)variance matrix. Residual effects consisted of all other genetic and non-genetic effects, except for the declared fixed effect (sub-plots); consequently, dominance or epistatic effects were pooled with genotype × environment interaction and micro-environmental effects into the residual effects. Other genetic models could be developed with REML VCE, such as the 'sire-dam' model in which a genotype is described by the average additive effect of its parents, or more complex models involving nested effects, genetic groups or maternal effects. But the simple individual model described above was more adapted to the present unbalanced data set.

Narrow-sense heritabilities were first estimated for each trait independently. Then a multiple-trait estimation was performed for the normally distributed traits (see below). Since it was not possible computationally to analyse the eight traits simultaneously, only six-trait analyses were made. Among the 28 possible combinations of six traits (among eight), eight combinations were chosen, giving a good coverage of possible combinations; these eight different combinations of six traits gave six estimates of heritability for each trait, and four to five estimates of each two-trait correlation. In each case, the mean estimate was computed, since the different estimated values were extremely similar from one six-trait-combination to another.

Comparison of the results with simple ANOVA

For each trait, a simple analysis of variance was performed to estimate the heritability without any consideration of the detailed pedigree information. The objective was to compare the results obtained from REML VCE with those obtained from this more simple methodology. After adjusting the data on plot (or sub-plot) effect, a one-way analysis of variance was performed by considering only the family level with the following simple model:

$$Y_{ij} = \mu + Fi + eij,$$

where i is the index of the family effect (Fi), and j is the index of the within-family individual effect (i.e. the residual effect: eij). Since all (except three) were full-sib families, the estimation of the narrow-sense heritability was computed as follows, with the hypothesis of neither dominance nor epistatic effects: $h^2 = 2\sigma^2_F/\sigma^2_P$, where σ^2_F is the between-family variance, and σ^2_P is the phenotypic variance. In a panmictic population, $\sigma^2_F = \frac{1}{2} * VA$ (additive variance) in the case of neither dominance nor epistasis, and if parents of the full-sib families are non-inbred and non-related. It is clearly not the case in the present apple-breeding population, but such an estimate was computed for comparison purposes.

Results

The mean, standard deviation and coefficient of variation of each trait have been computed from the raw data of the individual genotypes of the 213 families (Table 3). Similarly, phenotypic correlations between traits are given in Table 5. The frequency distribution of seven traits (SIZ, ATT, TEX, FLA, JUI, CIR, POW) were normal or approximately normal (e.g. Fig. 2A). Such normal distributions were in accordance with the quantitative features of these traits. For traits RUS, CRA, WAX, BUR, the frequency distribution showed a L-shape (e.g. Fig. 2B), which was expected in respect of the qualitative features of the traits (i.e. absence *versus* presence of the characteristic, with different levels of intensity when present). Most of the genotypes exhibited an absence of the target characteristics. These

Table 3 Basic statistics for the 11 traits analysed. For each trait: total number of hybrids assessed in the field, minimum and maximum values of the grading scale (except for CIR: in cm), mean value, standard deviation and coefficient of variation

Trait	SIZ	ATT	TEX	FLA	JUI	RUS	CIR	POW	CRA	WAX	BUR
No. genotypes	11 465	11 464	8590	8593	8587	11 461	11 431	12 900	11 458	11 276	11 050
Min.	1	1	2	1	2	1	113	1	1	1	1
Max.	4	5	4	5	4.5	4	460	5	4	4	4
Mean	2.09	2.56	2.55	2.58	2.94	1.97	268.8	2.46	1.44	1.17	1.38
SD	0.67	0.65	0.46	0.60	0.56	1.05	48.2	0.95	0.88	0.54	0.76
CV(%)	32	25	18	23	19	54	18	38	61	46	55

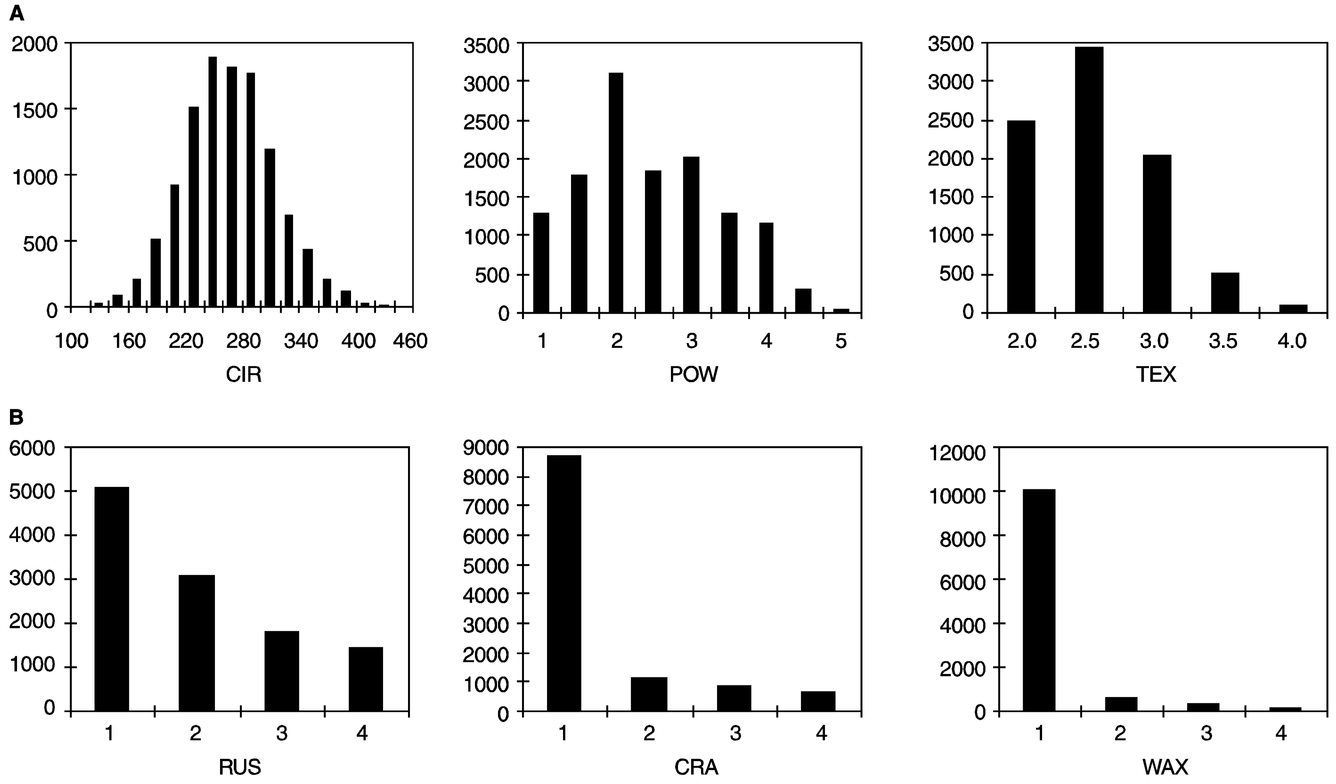

Fig. 2A, B Frequency distribution of several traits. **A** Traits with a normal or approximately normal distribution (*CIR*: trunk circumference, *POW*: powdery mildew resistance, *TEX*: fruit texture). **B** Traits with an L-shape distribution (*RUS*: fruit russeting, *CRA*: fruit cracking, *WAX*: waxiness of the fruit skin)

last traits (‘L-shape’ group) were considered apart from the previous ones in the following analyses, except for RUS which was clustered with the ‘normal’ group (Table 2). Of course, the standard deviations and phenotypic correlations involving traits of the L-shape group were extremely biased because of the nature of its distribution.

Inbreeding coefficients were computed by the software REML VCE from the whole-pedigree information (progenies, parents and ancestors): the average inbreeding coefficient was $F = 0.07$, whereas the maximum value was reached for only four individuals ($F = 0.50$); additionally only 6.5% of the individuals had an inbreeding coefficient equal to or higher than $F = 0.15$. The low value of the average inbreeding coefficient avoided potential interference between inbreeding and genetic-parameter estimations. Moreover, under the assumption of an infinitesimal model, even a high inbreeding level does not bias these estimations.

Heritabilities

Narrow-sense heritabilities estimated with REML VCE for each trait independently are given in Table 4. Heritability values ranged from 0.22 to 0.78. The vigour of the tree, evaluated by CIR, showed a high heritability (0.53). The size of the fruit (SIZ) and the fruit-quality traits (TEX, FLA, JUI) had medium heritabilities, from 0.33 to 0.39, as did the fruit-appearance traits (ATT, RUS). Resistance to powdery mildew appeared very heritable (0.68). Because of the large number of progenies, standard errors were low, around 0.03–0.05. Heritabilities of L-shape traits ranged from a low value (0.22 for CRA) to a very high value (0.78 for BUR).

A multiple-trait estimation was performed for the ‘normal’ traits (SIZ, ATT, TEX, FLA, JUI, CIR, POW, RUS): the mean estimates, computed over the eight combinations of six among eight traits (see Materials and methods), are given in Table 4. Heritabilities estimated through multiple-trait analyses were generally in very good agreement with those estimated independently, as described above. The higher discrepancy was observed for the juice score of fruit (JUI): the heritability increased from 0.34 (independent) to 0.39 (multi-trait), because of the rather high correlations between this trait and several others (see below). The standard deviations of the estimates were rather low both for single-trait and multi-trait estimations (Table 4). In each case, the multi-trait estimation was logically more precise than the single-trait estimation (from 0.025 to 0.056 for single-trait estimations, and from 0.018 to 0.027 for multi-trait estimations).

The heritability estimations obtained by analyses of variance (see Materials and methods) gave much lower values than those obtained by REML VCE (Table 4):

Table 4 Narrow-sense heritability estimation for each trait. Estimations were obtained with REML VCE for each trait independently (Single trait) and from a multiple-trait analysis (Multi-trait). Standard deviations computed by the software are indicated [SD(h^2)]. Estimations obtained from simple analyses of variance are also given (ANOVA)

Trait	SIZ	ATT	TEX	FLA	JUI	CIR	POW	RUS	CRA	WAX	BUR
Single trait:											
h^2	**0.33**	**0.37**	**0.33**	**0.39**	**0.34**	**0.53**	**0.68**	**0.36**	**0.22**	**0.36**	**0.78**
SD(h^2)	0.046	0.034	0.031	0.037	0.035	0.050	0.034	0.035	0.025	0.053	0.056
Multi-trait:											
h^2	**0.34**	**0.38**	**0.34**	**0.39**	**0.39**	**0.51**	**0.68**	**0.35**	/	/	/
SD(h^2)	0.027	0.022	0.022	0.025	0.027	0.019	0.024	0.018	/	/	/
ANOVA:											
h^2	**0.12**	**0.18**	**0.22**	**0.21**	**0.20**	**0.25**	**0.49**	**0.25**	**0.13**	**0.18**	**0.36**

Table 5 Correlation coefficient matrix between traits: phenotypic correlations (left-down side) and additive genetic correlations (right-up side, in bold)

Trait	SIZ	ATT	TEX	FLA	JUI	CIR	POW	RUS
SIZ	/	**0.59**	**0.29**	**0.43**	**0.68**	**0.29**	**0.13**	**– 0.09**
ATT	0.34	/	**0.45**	**0.45**	**0.68**	**0.15**	**0.30**	**– 0.40**
TEX	0.14	0.29	/	**0.87**	**0.73**	**– 0.13**	**0.24**	**0.14**
FLA	0.12	0.31	0.62	/	**0.74**	**– 0.07**	**0.26**	**0.17**
JUI	0.21	0.37	0.54	0.47	/	**0.10**	**0.18**	**– 0.12**
CIR	0.26	0.12	0.07	0.01	0.03	/	**– 0.26**	**– 0.12**
POW	– 0.05	0.08	0.02	0.03	0.08	– 0.17	/	**– 0.10**
RUS	– 0.18	– 0.48	– 0.03	– 0.01	– 0.09	– 0.13	– 0.00	/

the values ranged from 0.12 (SIZ) to 0.49 (POW), thus corresponding to only 35–72% of the REML VCE estimates.

Phenotypic and genetic correlations

Phenotypic correlations between traits were generally low to moderate (Table 5). The higher correlations were observed between the three fruit-quality traits (TEX, FLA, JUI) and ranged from 0.47 to 0.62. The fruit attractiveness (ATT) was correlated with the three previous quality traits (r around 0.30); logically, ATT and RUS (russeting) were negatively correlated ($r = -0.48$). The fruit size (SIZ) was moderately correlated with ATT, CIR and JUI.

The additive genetic correlations were estimated with the same eight combinations of six traits as described for the heritability estimation; the mean values are given in Table 5. For each pair of traits, the different estimates of the genetic correlation were very similar from one six-trait-combination to another, except for low values of genetic correlation ($|\rho_g| < 0.15$) where a greater variation was observed: e.g. ρ_g ranged from -0.034 to -0.095 between FLA and CIR (mean value: $\rho_g = -0.068$).

The estimated values of additive genetic correlations ranged from 0.07 to 0.87, in absolute values. Very high genetic correlations were observed between the three fruit-quality traits (TEX, FLA, JUI); these correlations were higher than those observed at the phenotypic level between the same traits. Fruit size (SIZ) was strongly correlated with the juice content (JUI, $\rho_g = 0.68$) and with fruit attractiveness (ATT, $\rho_g = 0.59$). It was moderately correlated with FLA, TEX and trunk circumference (CIR). ATT was strongly correlated with the three fruit-quality traits, especially with JUI ($\rho_g = 0.68$), and more logically with russeting (RUS, $\rho_g = -0.40$). CIR and POW (powdery mildew resistance score) were poorly correlated with other traits.

The standard deviation estimated for each correlation ranged from 0.018 to 0.062 depending on the two-trait combinations (data not shown). Higher standard deviations (from 0.04 to 0.06) were observed for genetic correlations involving SIZ, ATT, RUS and CIR.

Discussion

Individual model for apple-breeding data

In plants, genetic parameters of agronomical traits have rarely been estimated with an 'individual model' methodology. We report here the first study, to our knowledge, concerning such estimations within a whole breeding population where several generations have been traced (up to seven generations). Apple breeding data would have been very difficult to use for genetic parameter estimations without an individual model and the availability of the REML VCE software. The parents used for apple-breeding purposes were highly related through complex pedigrees; the prerequisites for traditional genetic analyses in plants (unrelated parents in balanced designs) were impossible to reach here. The heritability values obtained by simple analyses of variance were always underestimated (Table 4), mainly because the numerous relationships among parents were not taken into account. Conversely, the genetic parameters estimated by REML VCE corresponded to those of the founding population, i.e. the base unselected population which consisted of the oldest ancestors of the breeding population (see for example Fig. 1). Indeed, the relationship matrix was accounted for in the REML procedure to provide heritability estimations of this founding population, and not those of the last breeding generation. Such estimations are more favourable to further compute the BLUP of the genotypes (Henderson 1975).

Moreover, very few connections existed between experimental plots at the family level (see Materials and methods), so the whole data set was difficult to exploit with simple analyses of variance; the data were only adjusted on sub-plots prior to running the analyses of variance. Conversely, the individual model was able to design numerous connections among plots and subplots at higher generations, because of the complex and interconnected pedigrees (e.g. Golden Delicious or McIntosh were used as parents in one plot, as grandparents in another plot, as higher ancestors in yet another one, and so on). Such a better partition between plot effects and genetic effects in the individual model was also a very favourable point to improve the heritability estimations in comparison with a simple ANOVA.

Limits of the obtained results

The present data set also contained several drawbacks mainly concerning the scored traits, the data and experimental design, and the selection phases. The majority of the traits involved in this study were ordinal traits assessed on a grading scale which is less precise than a continuous quantitative assessment, especially because of the subjectivity of the observer. Variation in the trait assessment cannot be completely avoided, especially from year to year. Such background effects reduced the heritability estimation; conversely, the estimates obtained expressed the actual limits of such grading scales for selection purposes.

As described in the Materials and methods, these apple-breeding data were not initially designed for such an analysis of genetic parameters. The main purpose of the breeding programme was the creation of new apple cultivars by crossing traditional cultivars, or newly created hybrids, for further breeding purposes in the field. Within a sub-plot, the families were distributed in a single row and not randomly, which is unfavourable for genetic analysis. Here again, the ability of the individual model to produce connections among families and plots, because of the interconnected pedigrees, was a very favourable compensation.

When considering the whole apple-breeding population, numerous selection steps were applied both during the past breeding generations and within the last generation assessed in the field. During the past breeding generations, a high selection pressure was successively applied at each generation for the selection of new hybrids: e.g. X4972 (in Fig. 1) was selected on several agronomic traits within the cross Florina × Prima and was not a random representative offspring of its two parents. Such a selection pressure may have biased the estimations of genetic parameters by modifying the genetic relatedness in the studied population. Since the selection data were not available for the present analysis, it could not be accounted for by the REML procedure. Within the last breeding generation, two selection steps were performed prior to planting to discard within each progeny the individuals which were susceptible first to scab and then to powdery mildew (see Materials and methods). Such selection steps were not taken into account by the maximum-likelihood procedure, since the selection data were binary (resistant *versus* susceptible) and so non-informative. But the impact of scab and powdery mildew selections on the genetic-parameter estimation of the other traits may be considered as negligible, since no major effect of the disease resistance status of a genotype on its agronomical performance has been reported in the literature. Regarding the powdery mildew resistance assessed in the field, heritability estimation was probably much biased because of the nursery selection. But the correlation between nursery and field for mildew resistance is known to be rather moderate (Janse et al. 1994); hence the selection impact was difficult to assess and was probably variable from one progeny to another. The last selection step was performed during the scoring period on the planted progenies, since the fruit-quality traits were not assessed on the individuals showing a very poor fruit attractiveness (ATT) and/or a too small fruit size (SIZ). The selection rate was not severe (75%). Such a selection could be partly taken into account by the maximum-likelihood procedure of REML VCE, since the selection data were available (i.e. the discarded individuals with very poor fruit appearance or size were scored for such traits).

Even if some of the selection phases described above could have biased the estimation of the genetic parameters in this breeding population, the values obtained here are much more informative for future breeding purposes than any other estimates that could be obtained by more standard methodologies in plant breeding. Especially, the ability to take into account all the complex pedigree data of the breeding population is a very favourable point, as is the ability to build 'bridges' between sub-plots through these relationships. Since many apple breeders around the world are working with very similar plant material (Laurens 1998), these results may be generalized to many breeding populations.

Analysis of the results and comparison with previous inheritance studies

Taking into account the above advantages and drawbacks of the available methodology and data, several points can be underlined as regards the results. The heritability values obtained here were moderate to high for the normal traits, despite the imprecise scoring scales in classes (except for CIR). Heritability values of 0.3–0.4 are rather favourable and should guarantee the efficiency of mass selection in the field, especially for very important traits such as fruit quality (TEX, FLA, JUI) or fruit attractiveness (ATT). Such traits are most probably under the control of many genes with different effects (polygenic traits). Conversely, the high heritability value of POW could probably come from an oligogenic origin, where few genes influence the main part of the genetic variation. Regarding L-shape traits, BUR appeared to be much more heritable than CRA or WAX, which are most probably highly influenced by environmental factors; but much caution is necessary because of the non-normal distribution of these traits which biased the heritability estimation.

Regarding the genetic correlations between traits, a noticeable feature was the very high correlation structure among the three fruit-quality traits (TEX, FLA, JUI). These three traits may be controlled by genes which are either clustered in the genome or else have pleiotropic effects. But an over-estimation of these correlations could come from the scoring procedure since the three traits were assessed at the same time through a subjective evaluation. Other correlations could be explained by the traits themselves: the juice content (JUI) was logically highly correlated with the fruit size (SIZ), since small fruits gave much less juice (at least at a sensory level) than big fruits. Also, SIZ was highly correlated with fruit attractiveness, probably because of a subjective favourable influence of large fruit size on fruit-attractiveness scoring. Conversely, some genetic-correlation estimations were more questionable, especially those observed between fruit attractiveness and fruit-quality traits.

Few studies have been published on genetic parameters of agronomic traits in apple, mainly because experimental data from major breeding programmes were not suited for such estimations. In some cases, narrow-sense heritabilities were estimated from the linear regression of offspring performance on the average performance of their parents, or mid-parent value (Falconer 1981); in other cases, half-diallel mating designs were involved. Brown (1960) produced data which allowed the estimation of a much higher heritability for fruit size (around 0.60) than obtained here, probably because his scoring scale was more precise. Dathe (1978, 1979, 1980, 1984, 1985) analysed the data from a partial 14 × 14 half-diallel and obtained the heritability values or inheritance patterns of many morphological and agronomical traits: more particularly, she obtained a medium value of narrow-sense heritability for mildew susceptibility ($h^2 = 0.49$) and a high inheritance for yield and fruit size, involving mainly additive genetic effects (no estimated heritability). In a 8 × 8 half-diallel, Gelvonauskis (1994) estimated an heritability value for trunk diameter (0.43) very similar to the present CIR heritability. Conversely, he obtained a very low value for mildew resistance ($h^2 = 0.17$, instead of 0.68 here). But his data were recorded on juvenile seedlings instead of adult trees. Recently, Tancred et al. (1995) obtained a very high estimated value for narrow-sense heritability of the ripening date (0.94) by parent-offspring regression. Globally, it seems that additive factors are much more important than non-additive ones (dominance and epistasis) in the total genetic variance of most apple agronomic traits (Dathe 1978; Watkins and Spangelo 1970; Visser 1976; Gelvonauskis 1994; Tancred et al. 1995). The same appears to be true in pear (Thibault et al. 1988; Bell and Janick 1990; Abe et al. 1995).

Even if additivity is the major part of the total genetic variance in apple, interaction effects cannot be neglected for apple breeding, especially because only extreme genotypes will be favourable candidates for variety creation. Indeed, only a very favourable combination of numerous agronomic traits allows a genotype to become a commercialised cultivar. In such a context, dominance and epistatic effects would be interesting to assess. A specific mating design, such as a diallel, combined with an experimental design containing both parents and offspring in a similar physiological status (e.g. grafted onto the same rootstock at the adult stage), would allow the evaluation of both dominance and epistatic effects.

In the present paper, genetic parameters were obtained with an individual-model methodology in a large apple-breeding population. In a second step, these parameters will be useful to evaluate the breeding values (general combining abilities) of the major apple cultivars involved in the population, such as Golden Delicious, Red Delicious, Rome Beauty and many other traditional cultivars. The breeding values are interesting mainly to classify these cultivars in terms of the different agronomic traits which have been assessed. Also, the breeding values of recently selected hybrids which have still not been much used in crosses will be predicted; such information should be very valuable to design future crosses which favourably combine such promising hybrids within one another or with more traditional cultivars.

Acknowledgements We thank E. Groeneveld for providing the software. We are grateful to D. Boichard for scientific assistance. We also thank A. Rouillard for technical assistance, J. D. Flick for the database management, and E. Chevreau and J. Kervella for reviewing the manuscript.

References

Abe K, Sato Y, Saito T, Kurihara A, Kotobuki K (1995) Narrow-sense heritability of fruit characters in Japanese pear (*Pyrus pyrifolia* Nakai). Japan J Breed 45 : 1–5

Bell RL, Janick J (1990) Quantitative genetic analysis of fruit quality in pear. J Am Soc Hort Sci 115 : 829–834

Brown AG (1960) The inheritance of shape, size and season of ripening in progenies of the cultivated apple. Euphytica 9 : 327–337

Brown SK (1992) Genetics of apple. Plant Breed Rev 3 : 333–365

Chambers JM, Hastie TJ (1992) Statistical models in S. In: Wadsworth, Brooks (eds) Cole Advanced Books and Software, Pacific Grove, California

Crosby JA, Janick J, Pecknold PC, Korban SS, O'Connor PA, Ries SM, Goffreda JC, Voordeckers A (1992) Breeding apples for scab resistance: 1945–1990. Fruit Var J 46 : 145–166

Dathe B (1978) Quantitativ-genetische untersuchungen an apfelsämlingen zur entwicklung neuer selektionsprinzipien. Arch Züchtungsforsch 8 : 79–89

Dathe B (1979) Erste ergebnisse quantitativ genetischer untersuchungen an apfelsämlingen unter besonderer berücksichtigung der anfälligkeit gegenüber mehltau (*Podosphaera leucotricha*). Tagungsbericht (Akad Landwirtsch-Wiss DDR) 174 : 91–96

Dathe B (1980) Beitrag über die vererbung der frostempfindlichkeit reproduktiver organe bei apfel. Arch Gartenbau 28 : 465–472

Dathe B (1984) Beitrag zur züchtung auf ertrag bei apfel. Arch Gartenbau 63 : 245–256

Dathe B (1985) Genetische zwerge in kreuzungsnachkommenschaften von apfelsorten und möglichkeiten ihrer nutzung. Arch Gartenbau 33 : 497–511

Ducos A, Bidanel JP, Ducrocq V, Boichard D, Groeneveld E (1993) Multivariate restricted maximum-likelihood estimation of genetic parameters for growth, carcass and meat quality traits in French Large White and French Landrace pigs. Genet Selec Evol 25 : 475–493

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, London

Gelvonauskis B (1994) Inheritance of resistance to fungal diseases, morphological characters and combining ability in juvenile apple seedlings. Zemes Ukio Mokslai (Lithuanian Academy of Sciences) 2 : 61–66

Groeneveld E (1991) Simultaneous REML estimation of 60 covariance components in an animal model with missing values using the Downhill Simplex algorithm. In: Proc 42th Annu Meet Europ Assoc Anim Prod, Berlin, Germany, pp 108–109

Groeneveld E (1996) REML VCE, a multivariate multi-model restricted maximum-likelihood (co)variance component estimation package – Version 3.2, User's guide. Institute of Animal Husbandry and Animal Ethology, FAL, Neustadt, Germany

Henderson CR (1975) Best linear unbiased estimation and prediction under a selection model. Biometrics 31 : 423–447

Hough LF, Shay JR, Dayton DF (1953) Apple scab resistance from *Malus floribunda* Sieb. Proc Am Soc Hort Sci 62 : 341–347

Janse J, Verhaegh JJ, den Nijs APM (1994) Early selection for partial resistance to powdery mildew, *Podosphaera leucotricha* (Ell. et Ev.) Salm. in apple progenies. Euphytica 77 : 7–9

Laurens F (1994) Stratégies génétiques pour créer des variétés de pommier (*Malus* × *domestica*) résistant durablement à la tavelure (*Venturia inaequalis*). In: Proc Coll INRA-CTIFL Recherches Fruitières, Angers, France, pp 55–66

Laurens F (1998) Review on the current apple breeding programmes in the world: breeding objectives for scion-cultivar improvement. In: Proc EUCARPIA Fruit Breed Genet Symp, Oxford, England, *Acta Hortic* (in press)

Lespinasse Y (1989) Breeding pome fruits with stable resistance to diseases. 3. Genes, resistance mechanisms, present work and prospects. In: Gessler C, Butt J, Koller B (eds), Colloque OILB integrated control of pome fruit diseases, vol. II, pp 100–115

Lespinasse Y (1992) Le pommier. In: Gallais A, Bannerot H (eds) Amélioration des espèces végétales cultivées: objectifs et critères de sélection. Masson, Paris, pp 580–592

Lespinasse Y, Godicheau M, Olivier JM (1979) Etudes entreprises dans le cadre de la résistance à la tavelure du pommier. In: Proc EUCARPIA Fruit Section Symp Tree Fruit Breed, Angers, France, pp 97–110

Noiton DAM, Alspach PA (1996) Founding clones, inbreeding, coancestry, and status number of modern apple cultivars. J Am Soc Hort Sci 121 : 773–782

Noiton DAM, Shelbourne CJA (1992) Quantitative genetics in an apple breeding strategy. Euphytica 60 : 213–219

Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. Biometrika 58 : 545–554

Quaas RL (1976) Computing the diagonal elements and the inverse of a large numerator relationship matrix. Biometrics 32 : 949–953

Quaas RL, Pollak EJ (1980) Mixed-model methodology for farm and ranch beef cattle testing programs. J Anim Sci 51 : 1277–1287

Tancred SJ, Zeppa AG, Cooper M, Stringer JK (1995) Heritability and patterns of inheritance of the ripening date of apples. HortScience 30 : 325–328

Thibault B, Hermann L, Belouin A, Mangin B (1988) Inheritance of some agronomical traits in pear. Acta Hortic 224 : 199–209

Tixier-Boichard M, Boichard D, Groeneveld E, Bordas A (1995) Restricted maximum-likelihood estimates of genetic parameters of adult male and female Rhode Island red chickens divergently selected for residual feed consumption. Poultry Sci 74 : 1245–1252

Visser T (1976) A comparison of apple and pear seedlings with reference to the juvenile period. II. Mode of inheritance. Euphytica 25 : 339–342

Watkins R, Spangelo LPS (1970) Components of genetic variance for plant survival and vigor of apple trees. Theor Appl Genet 40 : 195–203

Williams EB, Dayton DF, Shay JR (1966) Allelic genes in *Malus* for resistance to *Venturia inaequalis*. Proc Am Soc Hort Sci 88 : 52–56