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ORIGINAL PAPER

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Genetic variance and breeding values for resistance to a wind-borne disease [*Sphaerotheca macularis* (Wallr. ex Fr.)] in strawberry (*Fragaria* × *ananassa* Duch.) estimated by exploring mixed and spatial models and pedigree information

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Abstract A mixed model approach was used to estimate variance components and heritabilities for resistance to powdery mildew, a wind-borne disease in strawberry. In order to improve precision in the statistical computations, spatial error control effects were included to account for systematic environmental variations in the large field trials. Pedigree information was included where feasible. Seedling families obtained from an incomplete 63-by-63 diallel cross were grown at six locations and scored subjectively for mildew attack three times during the growing season. The 63 parents included both European and American cultivars as well as advanced selections from various breeding programmes. A total of 298 full-sib families were realized, including 26 reciprocal families. No reciprocal differences were found. On a plot-mean basis, the broad-sense heritability was found to be intermediate, $H^2 = 0.44–0.50$, depending on whether the pedigree information was included in the model or not. The increase was mainly due to a substantial increase in the additive variance component. Likewise, the narrow-sense heritability increased from $h^2 = 0.39$ to $h^2 = 0.45$ when the pedigree information was included, while the ratio of the specific combining ability variance to the general combining ability variance fell from 13% to 10%. The predicted breeding values of the 63 parents demonstrate that important cultivars such as Elsanta and Korona are unlikely to produce progenies with a high degree of resistance. On the other hand, the Norwegian cultivar Solprins, the Canadian cultivar Kent and the Italian cultivar Patty appeared to give highly resistant progeny. At the full-sib level, the estimated disease scores ranged from 1.15 (Kent × Induka) to 4.19 (Cavendish × Avanta), revealing a huge range of variation for powdery mildew resistance available for selection.

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Introduction

Powdery mildew [*Sphaerotheca macularis* (Wallr. ex Fr.)] presents a serious problem to the Scandinavian strawberry (*Fragaria* × *ananassa* Duch.) industry. In Scandinavian countries, the pathogen often reaches epidemic proportions before the fruit is harvested—unlike in the more southern European countries where this rarely happens—thereby necessitating the use of fungicides. However, the adverse reaction of the consumers and growers to the use of fungicides has prompted a search for alternative ways of handling this problem. Consequently, in the publicly funded Norwegian strawberry breeding programme, which is run by Graminor AS, the development of cultivars with a high level of resistance to powdery mildew is one of the prime objectives.

The cultivar Korona is economically a very important cultivar in the Scandinavian strawberry industry and was considered to be resistant to powdery mildew when introduced in 1983. However, this cultivar is now susceptible to severe powdery mildew attacks unless treated with fungicides. This erosion of resistance could be due to mutation(s) breaking down the resistance in the plant material, but this explanation is not very likely. A more probable clarification is recombination or mutation in the pathogen resulting in the production of new virulent strains. Therefore, if breeders wish to keep the disease level low in the future without using fungicides, they will have to focus continuously on breeding for resistance.

In order to breed for powdery mildew resistance, a knowledge of the genetic basis for this resistance is important as this has implications for the breeding strategy. The inheritance of powdery mildew in straw-

berry has been studied in several breeding populations with varying outcomes (e.g. Daubeny 1961; Hsu et al. 1969; Nelson et al. 1995; Simpson 1987). There appears to be an agreement that both additive and non-additive genetic variance components are important. Most of the studies demonstrate that the inheritance of resistance is complex, indicating that breeding has to rely on developing cultivars with resistance based on several genes. Hsu et al. (1969), however, attempted an analysis based on Mendelian segregation and claimed that the resistance depended on two additive genes for resistance. In addition, epistasis was assumed to have played a part.

In the study reported here, we have used spatial correction techniques in the analysis of data obtained from large field trials. These techniques have—to our knowledge—not been previously applied to horticultural data. Moreover, we have included the pedigree information in the computations of breeding values. This was also done by Durel et al. (1998) but has not yet become a widespread approach in horticultural breeding research.

The objectives of the present study were first to estimate the genetic variance components useful in describing the mode of inheritance of the powdery mildew resistance. Second, we wanted to rank parents in our breeding population for their capability of transferring resistance to their progenies (i.e. their breeding value).

Materials and methods

Plant material

The parental plant material was drawn from strawberry genotypes included in the Norwegian strawberry breeding programme's germplasm collection. During the winters of 1998 and 1999, an incomplete diallel was generated using 63 advanced selections and cultivars from various European and American sources. A total of 298 combinations were realized, including 26 reciprocals, to make up what could be viewed as an incomplete form of Griffing's (1956) method 3.

Seeds from the full-sib families were germinated in mist chambers before being transplanted to 54-pot VEFI flats. The seedlings were raised in the greenhouse for 3–4 weeks and subsequently transplanted to the fields. At the beginning of the nursing period, vaporized sulphur was used to control the powdery mildew. Prior to transplantation, however, this regime was relaxed to allow for the inoculum to establish on the plants while under optimal conditions in the greenhouse.

Field layout and observations

The seedlings were transplanted into two-replicated field plots in six fields at three NCRI (Norwegian Crop Research Institute, As, Norway) field stations. In 1998, three fields were established; one in Bodø (67°3′N, 14°E), one in Stjørdal (63°5′N, 11°E) and one in Grimstad (58°4′N, 8°E). In 1999, two fields were established in Stjørdal and one in Grimstad. The two experiments in Stjørdal in 1999 were approximately 7 km apart, one on a silty clay loam (Stjørdal-C) and one on a sandy loam (Stjørdal-S). In all of the experimental fields, each plot consisted of 25 seedlings from the same full-sib family. Each of the fields were planted as latinized row-column designs (Williams 1986) using the ALPHA+ software to optimize the layouts.

Standard growing regimes were used except for the powdery mildew spraying which was limited to one standard application each of penkonazol (Topas 100EC; Syngenta, Basel, Switzerland) and triforin (Saprol) before the fruit was mature. This constitutes about half of the dose used by the growers.

A growing system with plastic mulch and fertigation was used. A balanced nutrient solution containing 7.8 mmol N, 1 mmol P, and 4.6 mmol K per litre was applied in a 1:100 ratio to equal approximately the recommended 60 kg N ha^{-1} through the entire growing season.

Scoring of the mildew attack was done on a plot-mean basis during the fruiting seasons of 1999 and 2000 following Simpson's (1987) scale:

1. no visual symptoms;
2. slight leaf curling, no apparent mycelia;
3. leaf curling and mottling;
4. severe leaf curling; reddening and visible damage to lower leaf surface;
5. severe necrosis and some leaf death. The scores were made by the same person three times during the fruiting season: at first appearance of mature fruits, in the middle of the fruiting season and immediately after the fruiting season.

Statistical analyses

Spatial modelling

For the purpose of establishing a statistical model which accounted for both the treatment structure and the design structure, including the spatial variability, we generated a univariate dataset from the multivariate data. The chosen statistical model was subsequently used on the multivariate data set, and inferences regarding various genetic parameters were made with and without the pedigree information of the plant material included.

The univariate modelling data set was generated from the multivariate data set accounting for the covariance between the scores. Several covariance structures were fitted, and the selection between them was done using the Akaike's information criterion (Akaike 1974). The resulting data was used in the initial spatial modelling.

Following Gilmour et al. (1997), the error variance is split in two parts, **R**, a spatially dependent error matrix

and, η, a matrix accounting for the plot measurement errors, sometimes called the nugget variance. The spatially dependent error matrix is formed as $\mathbf{R} = \sigma_e^2[\sum_r \otimes \sum_c]$, where $\sum_r$ is the covariance matrix associated with the rows in the field layout, and $\sum_c$ is the covariance matrix associated with the columns. Direct multiplication ($\otimes$) of these matrices gives an error matrix ($\mathbf{R}$) accounting for all the error covariances in the field being analysed. In addition to the correlated errors, the approach of Gilmour et al. (1997) allows for the inclusion of linear and cubic trends across rows and columns.

When modelling each of the six data sets we followed these steps:

1. as a base model, the usual model for a replicated experiment with independent errors was applied;
2. next, dependence between adjacent plots was modelled through $\mathbf{R}$ using a two-dimensional separable auto-regressive spatial model of first order, often referred to as AR1 × AR1 (Gilmour et al. 1997);
3. subsequently, the 'nugget' effect was included;
4. finally, other fixed or random design or trend effects (e.g. linear or/and cubic trends) were added.

The significance of the AR1 × AR1 spatial error model and the inclusion of the nugget effect were evaluated using the likelihood ratio χ^2 (Self and Liang 1987), as were the random trend effects, for example, cubic splines across rows or columns (Verbyla et al. 1999). The fixed trend effects, such as linear trends across rows or columns, and the fixed effects, such as rows or columns, were evaluated partly by the accompanying *F*-statistic and partly by inspecting the variogram of the residuals. The variogram is essentially the complement of the spatial autocorrelation matrix, but it is easier to view and interpret. If there is no pattern to the residuals, the variogram is essentially flat. A pattern is evident if the variance of differences between residuals of plots that are spatially close tends to be lower than that between those that are far apart.

Having decided on which spatial models to use for each site, we ran a combined analysis for all the six sites using the combined residual variance matrix as the direct sum of the six residual matrices, $\mathbf{R}' = \oplus_{j=1}^{6} \mathbf{R}_j$. In addition, the appropriate linear and cubic trends were included. In the combined analysis, the results from the single-site analyses were used as starting values.

Modelling the design and treatment structure

Our prime objectives were to make general inferences about the variation in mildew resistance in strawberries, to rank the parents according to their ability to transmit mildew resistance to their progeny and finally to make specific inferences about the value of the tested full-sib families. This calls for elimination of the influence of effects that are of no interest in this context. Considering the effects of location and replication within location as fixed in the model will yield unbiased estimates of the breeding values and the variances. Thus, the statistical model will take the form of a mixed model involving both random and fixed effects.

The across site model was

$$Y = \mathbf{X}\beta + \mathbf{Z}_{\mathrm{GCA}}\mathbf{u}_{\mathrm{GCA}} + \mathbf{Z}_{\mathrm{SCA}}\mathbf{v}_{\mathrm{SCA}} + \mathbf{Z}_{\mathrm{GCA\times Site}}\mathbf{u}_{\mathrm{GCA\times Site}} + \mathbf{Z}_{\mathrm{SCA\times Site}}\mathbf{v}_{\mathrm{SCA\times Site}} + \mathbf{R}', \quad (1)$$

where Y is the vector of unadjusted observations. The **X**-matrix and **Z**-matrices are incidence matrices belonging to their respective component, β is a vector of fixed effects of site and replicates within sites, $\mathbf{u}_{\mathrm{GCA}}$ and $\mathbf{v}_{\mathrm{SCA}}$ are vectors of general combining ability (GCA) effects and specific combining ability (SCA) effects across the sites. In addition, interaction terms and the error matrix is presented in Eq. 1.

The random effects in the model were assumed to follow a multivariate distribution with means and variances defined by

$$\begin{bmatrix} \mathbf{u}_{\mathrm{GCA}} \\ \mathbf{v}_{\mathrm{SCA}} \\ \mathbf{u}_{\mathrm{GCA\times Site}} \\ \mathbf{v}_{\mathrm{SCA\times Site}} \\ \mathbf{e} \end{bmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{A}\sigma^2_{\mathrm{GCA}} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_f\sigma^2_{\mathrm{SCA}} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_s \otimes \mathbf{A}\sigma^2_{\mathrm{GCA\times Site}} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_s \otimes \mathbf{I}_f\sigma^2_{\mathrm{SCA\times Site}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}' \end{bmatrix} \right) \quad (2)$$

where $\mathbf{0}$ is a null matrix; $\mathbf{A}$ is either the identity matrix with the order of number of parents (i.e. 63) or the numerator relationship matrix which describes the additive genetic relationships among the same parents (Henderson 1984), depending on which analysis was done. $\mathbf{I}_f$ and $\mathbf{I}_s$ are identity matrices with order equal to f (the number of full-sib families), and s is the number of sites, respectively; σ^2_{GCA} is the general combining ability variance (i.e. the variance between array means of half-sib families), σ^2_{SCA} is the specific combining ability variance and $\mathbf{R}'$ is the matrix of errors consisting of a separate error sub-matrix for each of the sites defined previously.

Due to the limited number of seedlings and unrealized parental combinations, there was a high degree of unbalance within and between the experimental fields. In order to estimate variance components and rank the parents, restricted maximum likelihood (Patterson and Thompson 1971) and best linear unbiased predictors

(BLUPs) were computed. Selection of full-sib families for cloning and subsequent trialling was done by considering them as fixed. All the computations were done using ASREML software (Gilmour et al. 2002).

Estimating genetic parameters

Under the usual assumptions of a large random mating parental population with disomic inheritance and near-linkage equilibrium among gene loci, the σ^2_{GCA} and σ^2_{SCA} variance components estimated under the mixed model defined have the following genetic expectations (Lynch and Walsh 1998):

$$\sigma^2_{GCA} \approx \frac{1}{4}\sigma^2_A + \frac{1}{16}\sigma^2_{AA} + \frac{1}{64}\sigma^2_{AAA} + \cdots \quad (3)$$

$$\sigma^2_{SCA} \approx \frac{1}{4}\sigma^2_D + \frac{1}{8}\sigma^2_{AA} + \frac{1}{8}\sigma^2_{AD} + \cdots \quad (4)$$

From Eqs. 3 and 4 estimates of the additive and dominance genetic variance components can be obtained. The presence of reciprocal crosses provided the opportunity to test for differences between maternal and paternal half-sibs. A preliminary statistical analysis showed, however, that such differences were not significant. Thus, the genetic modelling was done according to Griffing's (1956) model 4 (one set of $F_1 - s$, but neither reciprocals nor parents included).

Narrow-sense heritability (h^2) for selection among parental genotypes was estimated on an entry-mean basis unbiased by genotype-environment interactions as

$$h^2 = \frac{V_A}{V_P} \approx \frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + 2\sigma^2_{GCA\times Site} + \sigma^2_{SCA\times Site} + \sum_{i=1}^{n}\sigma^2_e/n} \quad (5)$$

The broad-sense heritability (H^2) was estimated as

$$H^2 = \frac{V_G}{V_P} \approx \frac{2\sigma^2_{GCA} + \sigma^2_{SCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + 2\sigma^2_{GCA\times Site} + \sigma^2_{SCA\times Site} + \sum_{i=1}^{n}\sigma^2_e/n} \quad (6)$$

and the proportion of dominance variance to the total phenotypic variance as

$$d^2 = \frac{V_D}{V_P} \approx \frac{\sigma^2_{SCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + 2\sigma^2_{GCA\times Site} + \sigma^2_{SCA\times Site} + \sum_{i=1}^{n}\sigma^2_e/n} \quad (7)$$

where n is the number of sites included in the computations. These parameters, including their approximate standard errors, were computed with ASREML using linear combinations of the appropriate variance components.

Results and discussion

Spatial corrections

In the relatively large experimental fields used here the assumption of homogeneity within replicates and blocks will in most cases not hold. In addition to variation related to soil factors, wind may cause heterogeneity in infection levels of airborne pathogens such as powdery mildew. Simpson (1987) suggested using border areas to eliminate this effect. This kind of error control would probably work only for relatively small experiments. In larger experiments like ours, the border effect would be negligible in the central areas of the fields. Therefore, the methods for spatial error control advocated by (Gilmour et al. 1997) has been used here.

The data from Stjørdal-S in 2000 is used to illustrate the spatial modelling procedure. Without any spatial corrections apart from replications, a log likelihood (LL) of 25.16 and a residual variance of 0.1971 was obtained (Table 1). The systematic trends across the experimental field are obvious from the accompanying variogram presented in Fig. 1a. Inclusion of the two-dimensional separable auto-regressive spatial model (AR1 × AR1) improved both the LL-value (38.13) and the residual variance (0.1845). However, the variogram still had the systematic pattern (Fig. 1b), hence the model was expanded with both linear regressions and random splines across columns and rows. The improvement of the LL-value (41.44) and the residual variance (0.1365) can be taken only as an indication of a better fit since these values strictly speaking are comparable only when models with an equal number of fixed effects are compared. However, the variogram was improved significantly (Fig. 1c), thereby supporting inclusion of these effects in this model. Table 2 shows the spatial error control effects included in each of the six experimental fields following equivalent procedures.

Differences among localities

The differences in mildew scores between the six experimental sites (Table 3) were significant when compared with an F-test ($P < 0.0001$). The lowest mildew attack was observed in Bodø, the northernmost location, with an average disease score of 1.81, while the highest score (3.36) was observed on the sandy loam field in Stjørdal-S. The silty clay loam field in Stjørdal-C displayed a much lower disease score (2.46), while the disease scores at the southernmost location, Grimstad, were 2.36 and 2.77 in 1999 and 2000, respectively. The overall standard error of differences among the sites was 0.1044. The

Table 1 Log-likelihood (LL) and residual variances (σ^2) before and after spatial error modelling within each of the six experimental fields

Location and year of scoring	Before		After	
	σ^2	LL	σ^2	LL
Grimstad (1999)	0.1816	44.65	0.1602	47.87
Stjørdal (1999)	0.0648	196.64	0.0529	207.9
Bodø (1999)	0.1070	135.1	0.0907	137.0
Grimstad (2000)	0.1354	36.98	0.1349	37.39
Stjørdal-S (2000)	0.1971	25.16	0.1365	41.44
Stjørdal-C (2000)	0.1400	66.48	0.1272	77.31

differences between the various locations could be due to several location-specific factors. It is, however, of significance to notice the difference between the two nearby fields in Stjørdal in 2000. The fact that the two fields were located on different soils could be one explanation for the observed difference. However, it is well known that other environmental factors in addition to soil factors influence the level of mildew attacks. For instance, the development of the powdery mildew relies on the alternation between dry days and cool, humid nights. Our observations indicate that, despite the short distance between these two fields, the humidity at night was much lower on the silty clay loam site. The humidity conditions of the sandy loam field have been known to be high during summer nights due to a large river near by. This would favour the growth conditions of the mildew and is a possible explanation for the higher scores observed at this site.

Variance components and genetic parameters

Table 4 shows the variance components and the genetic parameters estimated from the full data set with the longitudinal data from all six experimental sites. Similar components for a subset of the data, excluding Bodø 1999 and Stjørdal 1999, were also computed. The rationale for excluding these two sites was the low averages and small residual variances observed there (Tables 1, 3). However, this manipulation only caused minor changes to the estimated variance components and the breeding values. Thus, the results presented here are based on observations from all six experimental sites.

A preliminary analysis ruled out reciprocal differences or maternal effects. Thus, the effect of whether a parent appeared as a male or a female was not significant in these data. In contrast, MacLachlan (1978) came to the opposite conclusion. The variance components between means of half-sib families (σ^2_{GCA}), the maternal-paternal interaction (σ^2_{SCA}), and the half-sib mean × site interaction ($\sigma^2_{GCA\times site}$) were all highly significant as judged by their component/standard error ratio (Table 4). The mildew resistance is clearly under genetic control with a broad-sense heritability of $H^2 = 0.44 - 0.50$. The narrow-sense heritability was estimated to $h^2 = 0.39 - 0.45$, indicating a fairly small proportion of dominance variance ($d^2 = 0.03$) relative to the total phenotypic variance. Or, in other words, the specific combining ability variance (SCA) amounts to 10–13% of the general combining ability variance (GCA) depending on whether the relationship matrix was included or not. Hence, the major contribution to the genetic variance is of additive origin, with a minor but significant non-additive component (SCA). This is in agreement with other studies of mildew resistance in strawberry (see MacLachlan 1978; McNicol and Gooding 1979; Nelson et al. 1995).

The cultivated strawberry (*F.* × *ananassa*) is a relatively young octoploid species derived from its parental species *F. virginiana* and *F. chiloensis*, both octoploids from the Americas (Sjulin and Dale 1987; Dale and Sjulin 1990), thus most of the available germplasm is expected to be related. This was addressed by including the available pedigree information in the computations. The inclusion of the pedigree information apparently had some effect on the estimated size of the variance components as when this information was included the additive variance component and the narrow-sense heritability were inflated substantially (Table 4). In addition, but beyond the scope of the present paper, the pedigree information is highly useful when looking for molecular marker-trait associations in multiple crosses. Another aspect of the fact that the cultivated strawberry is a young species with a quite narrow genetic background is an expectancy of an overabundance of homozygotes compared to the Hardy-Weinberg equilibrium. This has implications for the variance component estimates. It has been shown that in a closely related population with an abundance of homozygotes relative to heterozygotes, the additive component of variance will be inflated compared to a Hardy-Weinberg situation (Honne 2001).

Nelson et al. (1995) found that the distribution of genetic variance components changes with the infection level: Increasing the infection level seemed to result in an increased general combining ability variance relative to the specific combining ability variance. This was inter-

Table 2 The effects included in the final model in addition to the basic statistical model for spatial error control

Location and year of recording	AR1 × AR1	Lin (col)[a]	Lin (row)	Spl (col)	Spl (row)
Grimstad (1999)	+	+		+	
Stjørdal (1999)	+	+			+
Bodø (1999)	+	+	+		+
Grimstad (2000)	+				
Stjørda-S (2000)	+	+	+	+	+
Stjørdal-C (2000)	+	+			+

[a]Linear trends and splines across columns and rows

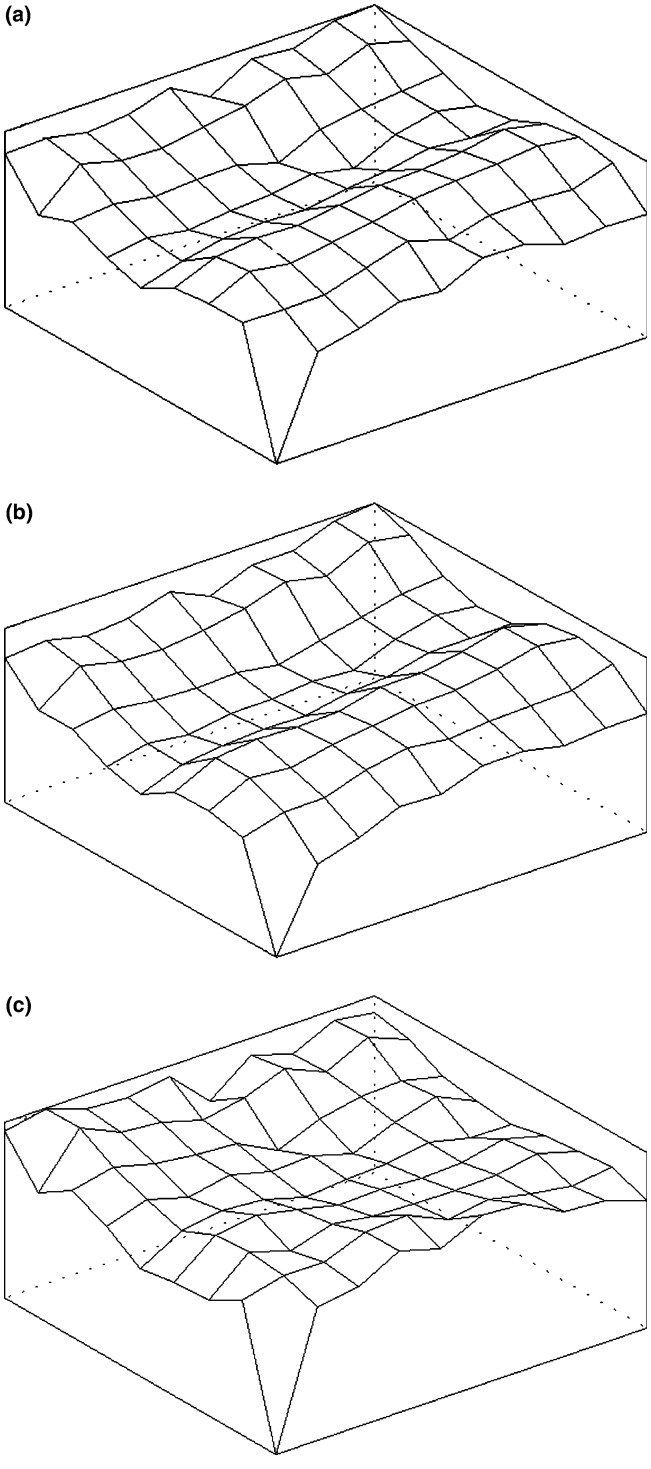

Fig. 1 **a**–**c** Variograms of residuals illustrating the model fitting process. **a** The variogram under a basic model without any additional spatial modelling. The variogram after including the separable auto-regressive spatial model (AR1 × AR1) is given in **b**. **c** The resulting variogram after including linear regressions and *splines* across *rows* and *columns*

preted as different genes conferring resistance depending on the infection level. It could, however, just be a matter of when the disease scores are made during a developmental continuum. Similar shifts in the distribution between the additive effects and dominance effects and the corresponding variances have been observed in several species (Breese 1969; Frandsen et al. 1978) during a developmental gradient.

Table 3 Predicted averages for the three periodic mildew scores at the six locations

Location and year of recording	First mildew score	Second mildew score	Third mildew score	Predicted average
Grimstad (1999)	2.25	2.38	2.45	2.36
Stjørdal (1999)	1.88	2.01	2.08	1.99
Bodø (1999)	1.70	1.83	1.90	1.81
Grimstad (2000)	2.66	2.77	2.86	2.77
Stjørdal-S (2000)	3.25	3.38	3.45	3.36
Stjørdal-C (2000)	2.35	2.48	2.55	2.46
	2.35	2.48	2.55	

The inferences made from the statistical parameters to the genetic parameters rely on, among other things, the fact that strawberry exhibits a disomic inheritance pattern. Based on cytological observations, several genomic formulas have been suggested for *F.* × *ananassa*. Bringhurst (1990) proposed a highly diploidized genome, and this has been supported by molecular studies of specific genomic regions (Arulsekar et al. 1981; Haymes et al. 1997). Lerceteau-Köhler et al. (2003), however, looked at a large number of amplified fragment length polymorphism (AFLP) markers and claimed that the meiotic behaviour is neither strictly polysomic nor disomic but something in between. Keeping in mind the short time span since *F.* × *ananassa* was synthesized, this explanation sounds plausible. Thus, there appears to be some controversy about the meiotic behaviour of strawberry. An irregular inheritance would have consequences on the inferences made on the genetic parameters. In such a case, the GCA variance will include non-additive elements and thus to some extent overestimate the additive variance (Gallais 1990).

In the present work, the hypothesis of Nelson et al. (1995) has not been explicitly addressed since all plants were infected equally in the greenhouse before being transplanted. Certainly, there was a small increase in the disease severity as the season progressed (Table 3). However, the estimated genetic variance components and heritabilities turned out to be fairly similar across the three sets of scores (not shown). Moreover, it appears that the rank correlations of the breeding values were consistently high among the various times of scoring. These correlations varied from 0.84 between the first and the third scores to 0.92 between the first and the second scores.

Breeding values of examined cultivars

The parents are ranked in Table 5 by their predicted breeding values pooled over all sets of scores. The rank

Table 4 Estimated variance components and their ratios to the standard error (SE) using longitudinal data from six locations including or excluding the pedigree information

Source	Without pedigree information		With pedigree information included	
	Variance component	Component/SE	Variance component	Component/SE
σ^2_{GCA}	0.1132	4.91	0.1455	4.88
σ^2_{SCA}	$0.1513E^{-1}$	4.14	$0.1515E^{-1}$	4.15
$\sigma^2_{GCA\times site}$	$0.1285E^{-1}$	4.67	$0.1407E^{-1}$	4.49
$\sigma^2_{SCA\times site}$	$0.4923E^{-2}$	1.17	$0.4972E^{-2}$	1.19
Residual[a]	0.3057		0.3056	
σ^2_A	0.4526	(0.092)	0.5822	(0.119)
σ^2_D	0.0601	(0.015)	0.0606	(0.015)
SCA/GCA	0.13	(0.043)	0.10	(0.034)
h^2	0.39	(0.049)	0.45	(0.051)
d^2	0.03	(0.007)	0.02	(0.006)
H^2	0.44	(0.046)	0.50	(0.048)

[a]Approximate standard errors of the genetic parameters are given within parentheses

shifts when the pedigree information was included were only minor. The best parents for transmitting mildew resistance are the Norwegian cultivar Solprins and the Canadian cultivar Kent, while the poorest are the Canadian cultivars St. Pierre and Cavendish. While otherwise highly useful parents such as Oka, Jonsok, Marmolada and Honeoye also proved valuable with respect to transmitting powdery mildew resistance, others such as Korona scored quite low (Table 5). This indicates that the susceptibility to powdery mildew observed in this cultivar by the industry has a clear genetic basis.

In Table 5, only genotypes used as parents in our breeding programme are presented. However, including the pedigree information also provides the possibility to predict the breeding values of genotypes where no data is available. In this case, the predictions will be based on relatives for which data exist. Secondary parental material for which we lacked direct data but which appeared to score high as donors of powdery mildew resistance were Irvine (-0.500 ± 0.285), Puget Beauty (-0.393 ± 0.287), Douglas (-0.357 ± 0.261), Muir (-0.312 ± 0.325), Brighton (-0.286 ± 0.296), Tufts (-0.283 ± 0.317) and Valentine (-0.271 ± 0.293). Based on our available pedigree information, Puget Beauty and Valentine are relatively unrelated, both to each other and to the rest of the mentioned cultivars. Thus, they stand out as two separate sources of resistance. Puget Beauty is one of the primary parents of both Totem and Induka (Table 5), while Valentine is found in the pedigrees of Solprins (twice), Patty and Oka.

Irvine, Douglas, Muir, Brighton and Tufts are highly related. Douglas and Muir are the primary parents of Irvine. Tufts is one of the primary parents of Douglas, and Tioga is one of the primary parents of Tufts. In addition, Tufts is one of the primary parents of Brighton, indicating that the high breeding value estimated for these cultivars originates from one common source. This trait has most likely been passed on through Tufts from either Tioga or the other primary parent of Tufts (CAL46.5.1). If we add fact that Tioga is found in the pedigree of cultivars such as Kent, Seascape, Carlsbad, Micmac and Sumas (Table 5), we are inclined to conclude that this source of powdery mildew resistance is Tioga.

Specific combining ability

Among the top five ranked full-sib families in Table 6, four have parents that also are ranked with high breeding values (Table 5). One of the parents of the fifth-ranked full-sib family (Symphony), however, is ranked as number 40 in Table 5, providing an example of the importance of the specific combining ability for the powdery mildew resistance. Another example can be seen directly from Table 5 where the Italian cultivar Patty is among the highest ranked, while its parents, Honeoye and Marmolada have breeding values close to the overall average.

Implications for breeding and cultivar development

The breeding material in the Norwegian strawberry breeding programme can be regarded as two separate but connected populations: a base population which is subjected to recurrent but relatively weak selection pressure, and a population for cultivar development, which is extracted from the base population.

The breeding values shown in Table 5 indicate which parents to use in order to increase the powdery mildew resistance in the next cycle of the recombined base population. Some examples of good specific combinations are also mentioned, and others are likely to exist bearing in mind that only a fraction of the 63-by-63 diallel cross was realized.

The cultivar development population consists of a limited number of top ranking full-sib families. These are subject to strong within-family selection in order to develop new potential cultivars. In fact, given Hardy-Weinberg equilibrium, one would theoretically expect a larger mean genetic variation within families than between families (Simmonds 1996). The possible excess of homozygotes compared to the Hardy-Weinberg equilibrium mentioned earlier would modify this. With

Table 5 Breeding values for the powdery mildew disease scores for the parents used in the NCRI strawberry-breeding programme

Examined primary parents	Secondary parents		Without the pedigree accounted for			With the pedigree accounted for		
	Maternal	Paternal	Breeding value of genotype	Standard error	Rank	Rank	Breeding value of genotype	Standard error
Solprins	Glima	Belrubi	−0.578	0.141	1	3	−0.548	0.162
Kent	(Redgauntlet × Tioga)	Raritan	−0.578	0.147	2	2	−0.550	0.162
Patty	Honeoye	Marmolada	−0.542	0.152	3	1	−0.563	0.164
ITA90.190.2[a]	ITA81.61.7	ITA79.114.4	−0.493	0.154	4	5	−0.493	0.174
Totem	Puget Beauty	Northwest	−0.479	0.093	5	6	−0.486	0.119
Oka	K75_13	Honeoye	−0.464	0.142	6	9	−0.410	0.161
Seascape	Selva	Douglas	−0.455	0.141	7	4	−0.503	0.158
Induka	Puget Beauty	Senga Sengana	−0.439	0.080	8	10	−0.404	0.109
Carlsbad	Irvine	CAL85.218.605	−0.423	0.093	9	7	−0.437	0.118
Laguna	Irvine	CAL85.92.602	−0.415	0.093	10	8	−0.432	0.117
Yamaska	Pandora	Bogota	−0.397	0.152	11	12	−0.374	0.169
Chandler	Douglas	CAL72.361.105	−0.358	0.097	12	13	−0.362	0.125
Anaheim	Irvine	CAL85.92.602	−0.346	0.121	13	11	−0.379	0.140
Micmac	Tioga	Guardsman (selfed)	−0.341	0.140	14	16	−0.327	0.157
Don	Brighton	CAL65.65.601	−0.315	0.154	15	15	−0.346	0.179
Selva	CAL70.3117	CAL71.98.605	−0.298	0.139	16	14	−0.360	0.156
Sumas	Cheam	Tioga	−0.246	0.096	17	17	−0.238	0.121
Jonsok	Senga Sengana	Valentine	−0.214	0.109	18	19	−0.183	0.131
Mohawk	MDUS4587	Earliglow	−0.202	0.098	19	20	−0.173	0.122
Tioga	Lassen	CAL42_8_16	−0.170	0.107	20	18	−0.205	0.131
St. Willams	Guardsman	V6747R_6	−0.109	0.207	21	21	−0.115	0.221
Governor Simcoe	Holiday	Guardsman	−0.075	0.091	22	23	−0.053	0.117
Honeoye	Vibrant	Holiday	−0.074	0.082	23	22	−0.059	0.110
Marmolada	Gorella	Sel15	−0.067	0.082	24	24	−0.051	0.110
Holiday	NY844	Raritan	−0.044	0.091	25	29	0.027	0.115
Puget Reliance	BC77.2.72	WSU1945	−0.012	0.098	26	25	−0.024	0.125
SJ8976-1	Chandler	Jewel	−0.003	0.088	27	27	0.001	0.114
Cuesta	Seascape	CAL83.25.2	0.009	0.088	28	28	0.002	0.114
Tenira	Redgauntlet	Gorella	0.020	0.080	29	32	0.066	0.109
Onda	ITA83.52.01	Marmolada	0.032	0.153	30	26	−0.019	0.168
Hapil	Gorella	Souvernir de Charles Machiroux	0.036	0.095	31	34	0.074	0.119
Oso Grande	Parker	CAL77.3.603	0.038	0.147	32	31	0.060	0.165
Camarosa	Douglas	CAL85.218.605	0.045	0.088	33	30	0.031	0.114
ITA80.52.1	Cardinal	ITA74.30.1	0.073	0.099	34	35	0.094	0.123
Pajaro	CAL63.7.101	Sequoia	0.074	0.093	35	33	0.066	0.117
Tamella	Gorella	Talisman	0.083	0.077	36	37	0.115	0.106
Latestar	Lateglow	Allstar	0.089	0.096	37	36	0.098	0.121
Symphony	Rhapsody	Holiday	0.097	0.092	38	40	0.130	0.117
Raritan	Redglow	Jerseybelle	0.118	0.095	39	41	0.149	0.121
Lateglow	Tamella	MDUS3184	0.119	0.096	40	43	0.165	0.122
Miss	Dana	ITA80.39.1	0.129	0.152	41	39	0.123	0.171
Scotland	Guardian	V6747R_6	0.133	0.094	42	42	0.149	0.119
Pegasus	Redgauntlet	Gorella	0.140	0.089	43	44	0.166	0.115
Elsanta	Gorella	Holiday	0.155	0.075	44	46	0.180	0.105
Northeaster	MDUS4380	Holiday	0.168	0.147	45	47	0.193	0.162
SJ8942-8	SJ8518.8	Jewel	0.187	0.104	46	48	0.220	0.127
ITA91.290.3	Honeoye	Marmolada	0.189	0.161	47	38	0.115	0.171
Bounty	Jerseybelle	Senga Sengana	0.203	0.088	48	49	0.221	0.114
ITA89.250.1	ITA83.5.8	Marmolada	0.231	0.152	49	45	0.174	0.168
Inga	(Nora × Korona)	(Viking × Elsanta)	0.241	0.102	50	50	0.275	0.126
Earliglow	(Fairland × Midland)	(Redglow × Surecrop)	0.277	0.095	51	51	0.285	0.124
Selkirk	Earlibelle	Holiday	0.296	0.096	52	52	0.325	0.120
Joliette	Jewel	SJ8518.9	0.309	0.082	53	53	0.334	0.109
Chambly	Sparkle	Honeoye	0.311	0.143	54	54	0.349	0.163
Senga Sengana	Sieger	Markee	0.320	0.109	55	56	0.370	0.128
Eros	Elsanta	Allstar	0.322	0.091	56	55	0.361	0.116
Jewel	(Senga Sengana × NY E 58)	Holiday	0.378	0.093	57	57	0.396	0.118
Korona	Tamella	Induka	0.453	0.117	58	58	0.458	0.134
Lambada	Sivetta × Holiday	Karina × Primella	0.481	0.143	59	59	0.548	0.163
Settler	Guardian	Holiday	0.531	0.095	60	60	0.556	0.121
Avanta	Induka × Sivetta	Karina × P d Romagna	0.599	0.086	61	61	0.608	0.114
Cavendish	Annapolis	Glooscap	0.605	0.147	62	62	0.632	0.164
St.Pierre	Chandler	Jewel	0.644	0.149	63	63	0.680	0.164

[a] Advanced selections from the Italian and the Quebec strawberry breeding programmes are labelled with prefixes ITA and SJ, respectively

Table 6 Predicted disease scores and the associated standard errors for the five top ranked and five bottom ranked full-sib families

Rank	Cross	Predicted disease score	Standard error[a]
1	Kent × Induka	1.15	0.276
2	Yamaska × Solprins	1.19	0.370
3	Oka × Anaheim	1.48	0.268
4	Yamaska × Micmac	1.57	0.277
5	Totem × Symphony	1.65	0.184
294	Miss × Korona	3.58	0.275
295	Chambly × Senga Sengana	3.67	0.277
296	ITA89.250.1 × Korona	3.70	0.279
297	Saint-Pierre × Avanta	4.18	0.277
298	Cavendish × Avanta	4.19	0.278

[a] The overall standard error was 0.309

increasing homozygosity in the parental population, the mean within-family variance decreases, while the among-family variance increases. Our own unpublished data indicate that in addition to the large variation among full-sib families there is a significant amount of variation within families. Consequently, selecting within the best full-sib families for cultivar development appears to be a reasonable strategy to maximize the probability of finding good genotypes. Among the 298 full-sib families evaluated in the experiments, the predicted disease scores varied from 1.15 (Kent × Induka) to 4.19 (Cavendish × Avanta). The five poorest and the five best ranked full-sib families are presented in Table 6, indicating a huge variation among families.

Our results indicate that it should be feasible to develop cultivars with increased resistance to powdery mildew. Whether this would be a lasting resistance one cannot say. The experience with powdery mildew in other crops (e.g. barley) implies that continuous breeding is required irrespective of what type of resistance genes have been used. Our growers' experience with the cultivar Korona, which has shown an increasing susceptibility to powdery mildew, supports this, while in other cases the resistance appears more durable.

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