



## Correlation between late blight resistance and foliage maturity type in potato

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### Summary

The genetics of race-non-specific foliage resistance against *Phytophthora infestans*, of foliage maturity type, and of their association in potato (*Solanum tuberosum*) were studied. Six progenies were derived from a half-diallel set of crosses between diploid potato clones that represented a broad pool within the genus *Solanum* and were free of any of the 11 known *R* genes for late blight resistance. The progenies were evaluated for resistance to late blight and for foliage maturity type, and five of them showed a significant correlation between the two traits. The correlation did not account for all variation that was present for both traits, as reflected in the analysis in which the relative AUDPC values were adjusted for foliage maturity type. The present study adds to previous results: resistance against *P. infestans* always coincides with late foliage maturity. However, the results also indicate that some selection for late blight resistance without affecting the foliage maturity type should be possible.

**Abbreviations:** AUDPC: area under the disease progress curve; GCA: general combining ability; SCA: specific combining ability

### Introduction

Breeding for foliage resistance against *Phytophthora infestans* in potato (*Solanum tuberosum*) started soon after the first late blight epidemics in Europe (1840s), and became successful with the introgression of race-specific resistance (*R*) genes from *S. demissum* (Müller & Black, 1952). The monogenic, dominant *R* genes with major effects on late blight resistance gained ground quickly, as introduction in the tetraploid potato crop was relatively easy (Umaerus, 1970). However, this race-specific approach has turned out not to be durable, because compatible races of *P. infestans* appeared rapidly and are now present for (combinations of) all 11 known *R* genes (Turkensteen, 1993). Current potato varieties carry subsets of these 11 *R* genes (Ross, 1986; Turkensteen, 1989), but their effectiveness is limited, since it depends on the unpre-

dictable racial composition of the pathogen population in the area of cultivation. Race-non-specific resistance to late blight in potato appears to be more durable, but provides only partial protection (Thurston, 1971). This type of resistance is characterized by a continuous variation in phenotypic appearance and a complex polygenic inheritance, which make breeding for this trait rather difficult (Umaerus, 1970). The uncertainty about the number of genes involved (Gebhardt & Valkonen, 2001; Simko, 2002) and the impossibility to indisputably prove race-non-specificity (Johnson, 1979) frustrate breeding for this type of late blight resistance. An additional difficulty is the association of race-non-specific resistance with late foliage maturity (Toxopeus, 1958), causing the virtual non-existence of early maturing potato varieties with satisfactory levels of resistance to late blight (Swiezynski, 1990).

The association between race-non-specific resistance against *P. infestans* and foliage maturity type in potato might be either genetic or physiological (Toxopeus, 1958). Physiological linkage is supported by observations that environmental conditions affect both traits. Most illustrative is the effect of photoperiod: short photoperiods reduce late blight resistance and simultaneously cause early foliage maturity (Pohjakallio et al., 1957; Umaerus, 1959). The presence of separable loci for the two traits seems improbable, as potato breeders have fruitlessly tried to combine resistance to late blight with early foliage maturity for decades (Muskens & Allefs, 2002). These breeding programmes involved production and testing of thousands of genotypes each year, a number most likely sufficiently large to reveal even the rarest recombinant if proper identification was feasible within the applied selection procedures. Recent molecular marker studies confirmed the association between the two traits once more: all loci for foliage maturity type coincide with loci for late blight resistance (Collins et al., 1999; Ewing et al., 2000; Oberhagemann et al., 1999). All these data seem to support a physiological linkage between race-non-specific resistance to late blight and foliage maturity type. However, the presence of genes with pleiotropic effects, or even different genes with different functions that are closely linked on the same loci, cannot be excluded yet (Visker et al., 2003).

The aim of the present research was to study the genetics of race-non-specific resistance against *P. infestans*, of foliage maturity type, and of their association in potato. Test crosses were made with diploid potato clones with different phenotypes for late blight resistance and foliage maturity type, that represented a broad pool within the genus *Solanum* and were free of any of the 11 known *R* genes for resistance to late blight. The offspring was evaluated in the field for

foliage resistance against *P. infestans* and for foliage maturity type.

## Materials and methods

### Plant material

Four diploid potato clones were used as parents in a half-diallel set of crosses. These parents were selected for their extreme phenotypes for foliage maturity type and foliage resistance to late blight, and comprised an early maturing, relatively resistant clone, two early susceptible clones, and a late resistant clone (Table 1). Clone I88.55.6 (I) was initially classified as late susceptible, but proved to be rather early in the present study. The parents were chosen because they were unrelated and no *S. demissum* was present in their pedigrees. These criteria were set to favour a broad gene pool and to avoid the presence of any of the 11 known *R* genes for resistance against *P. infestans*, respectively.

The half-diallel set of crosses was made in a greenhouse during the summer of 1998. This resulted in a total of five progenies that were randomly restricted to 300 genotypes each, and one progeny of 227 genotypes (Table 2). In spring 1999, seedlings of all genotypes were grown in a greenhouse and tubers were harvested in early summer. These harvested tubers were kept warm and humid (26 °C, RH 95%) for 2–4 weeks to break dormancy, and were planted in greenhouses for multiplication in autumn 1999. The parents were also included in this multiplication cycle. Tubers were harvested at the end of the year and kept at room temperature until planting the field-tests next spring. During the summer of the year 2000, material of progeny 5 (SH × CE, Table 2) and of the four parents was multiplied once more in a greenhouse, stored at 4 °C after harvest, and kept at room temperature for 4 weeks prior to planting the field-tests in spring 2001.

Table 1. Characteristics of the diploid potato clones used as parents of the half-diallel set of crosses. The phenotypic classification indicates foliage maturity type (Early and Late) and resistance against *P. infestans* (Resistant and Susceptible)

| Parent            | Phenotype         | Cross  | Source/Reference                                  |
|-------------------|-------------------|--|---|
| DH84-19-1659 (DH) | Early/resistant   | Prickle pollinated tetraploid <i>S. tuberosum</i>  | Plant Research International                      |
| SH82-44-111 (SH)  | Early/susceptible | Self-fertilised diploid <i>S. tuberosum</i>  | Colon et al. (1995), Sandbrink et al. (2000)      |
| I88.55.6 (I)      | Early/susceptible | ( <i>S. tuberosum</i> × <i>S. stenotomum</i> )<br>× ( <i>S. tuberosum</i> × <i>S. stenotomum</i> ) | Collins et al. (1999), Oberhagemann et al. (1999) |
| CE51 (CE)         | Late/resistant    | ( <i>S. phureja</i> × ( <i>S. vernei</i> × <i>S. tuberosum</i> ))                                  | Jacobs et al. (1995), Van Eck et al. (1995)       |

Table 2. Scheme of the half-diallel set of crosses with four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE), comprising six progenies with their selected numbers of offspring. For convenience, progenies are numbered 1 to 6, as indicated between brackets

| Female parent | Male parent |         |         |         |
|---------------|-------------|---------|---------|---------|
|               | DH          | SH      | I       | CE      |
| DH            | –           | 300 (1) | 300 (2) | 300 (3) |
| SH            |             | –       | 300 (4) | 227 (5) |
| I             |             |         | –       | 300 (6) |
| CE            |             |         |         | –       |

#### Field-tests for late blight resistance

All 1727 genotypes of the six progenies along with the four parents were evaluated for foliage resistance to late blight in the year 2000. Progeny 5 (SH × CE) and the four parents were tested again in 2001, in order to estimate year-effects. Evaluations of foliage maturity type were not performed in these fields, because assessment of the two traits on the same plants is not feasible. Both late blight resistance trials were located on sandy soil near Wageningen (The Netherlands) and consisted of three randomised blocks. Every genotype was present in a plot of two plants in each block; these two-plant plots were treated as single experimental units. The 2000 trial comprised five strips of 12 ridges each, and the 2001 trial two strips of 12 ridges each. The strips were bordered by single ridges of potato variety Irene, and separated from one another by paths of 2.25 m wide to allow tractor access. The two plants per plot were in the same ridge at a distance of 0.35 m; ridges were 0.75 m apart. Within ridges, the two-plant plots were alternated with single spreader plants of variety Nicola that is moderately susceptible to late blight. These spreader plants were included to maintain the production of late blight spores after the initial inoculation, in order to keep a continuous infection pressure during the period of disease assessments. Space for either one or two plants was left open between the plots and the spreader plants to allow access for evaluations (for details see, Colon & Budding, 1988). Four standard varieties (Eersteling, Bildtstar, Ostara, and Pimpernel) were included to monitor homogeneity of disease development over the field.

The 2000 experiment was planted on 19 April, treated with the herbicides Afarin (linuron) and Boxer (prosulphocarb) after planting, and with the insecticide Decis (deltamethrin) on 11 May and 26 June to con-

trol Colorado beetles. The 2001 trial was planted on 13 April, treated with the herbicides Linuron (linuron) and Boxer after planting, and with the insecticides Ambush (permethrin) on 26 June and Decis on 4 July. No fungicides were applied.

Plants were inoculated approximately 8 weeks after emergence (20 June 2000 and 18 June 2001) by spray application of a spore suspension of race 1.2.3.4.5.6.7.10.11 of *P. infestans* (IPO82001; Flier et al., 2003). The suspension was obtained by washing spores from leaves of varieties Bildtstar and Nicola that had been detached and inoculated 7 days prior to the field inoculation, and had been incubated in moist trays in a growth chamber. The concentration of the wash-suspension was  $1.5 \times 10^7$  zoospores plus  $2 \times 10^7$  sporangia per l in the year 2000, and  $1.4 \times 10^7$  zoospores plus  $2.3 \times 10^7$  sporangia per l in the year 2001. Plants and soil were thoroughly wetted prior to inoculation, and the spore suspension was applied late in the evening using a tractor-driven sprayer ( $7 \text{ ml m}^{-2}$ ). Subsequently, overhead irrigation was applied to sustain the development of the epidemic (as described by Colon & Budding (1988)).

In both years the first necrotic spots were visible 4 days after inoculation, and disease assessments were made over a period of 6 weeks thereafter at weekly intervals in the year 2000 (26 June–31 July) and twice a week in 2001 (25 June–30 July). The percentage of late blight-affected leaf tissue per plot was estimated using a scale comprising 16 classes, corresponding to 0, 0.5, 1, 5, 10, 20, ..., 80, 90, 95, 99, 99.9% of diseased leaf tissue (Colon & Budding, 1988). The disease ratings were used to calculate the normalised or relative area under the disease progress curve (AUDPC) (Fry, 1978; Shaner & Finney, 1977). Relative AUDPC values range between 0 and 1, and reflect both the onset and the rate of disease development, resulting in low values for resistant genotypes and high values for susceptible ones.

#### Field-tests for foliage maturity type

All genotypes and parents of the half-diallel set of crosses were evaluated for foliage maturity type in the year 2000. Progeny 5 (SH × CE) and the four parents were evaluated again in 2001. Both trials were situated on sandy soil in Wageningen (The Netherlands) and consisted of three randomised blocks. Each genotype was present in a plot of three plants per block, and plots were treated as single experimental units. The 2000 trial comprised four strips of eight ridges each; the 2001 trial one strip of 10 ridges. The strips were

bordered by single ridges of variety Irene and separated from one another by paths of 2.25 m wide. The three plants per plot were in the same ridge at a distance of 0.35 m, and ridges were 0.75 m apart. Within ridges, the three-plant plots were alternated with two open plant spaces to allow access for evaluations.

The 2000 trial was planted on 14 April, treated with Afarin and Boxer after planting, and with Decis on 19 June to control Colorado beetles. The fungicide Shirlan (fluazinam) was applied when necessary to prevent late blight infection. The 2001 experiment was planted on 23 April, treated with Linuron and Boxer after planting, and with Decis on 24 August. The fungicides Shirlan and Tattoo C (chlorothalonil, propamocarb-hydrochloride) were used to avoid late blight damage.

The procedure for evaluating foliage maturity type is less standardised, but is generally based on visual classification of senescence of the foliage once a season, at a distinct stage of senescence of a reference variety (Oberhagemann et al., 1999; Van Eck, 1995; Visker et al., 2003). The timing of the assessments is crucial, as differentiation of the genotypes is highly dependent on the amount of variation displayed at the moment of evaluation. In the present study, assessments of foliage maturity type were performed biweekly over a period of several months that started when the first symptoms of senescence were visible and ended at the first ground frost. This period ranged from the beginning of August until mid December in the year 2000, and from the end of July until the beginning of October in 2001. The summer of 2000 was considered normal with respect to temperature and amounts of sunshine and rain, whereas autumn was mild, dull, and wet. The summer of 2001 was warm, sunny, and wet, while autumn was very mild, normally sunny, and very wet (<http://www.knmi.nl>).

The assessments of foliage maturity type implied the visual classification of a whole syndrome of features representing foliage maturity. The most important components of this syndrome were sagging of the plants, termination of apical growth, and discoloration of the leaves. Assessments were recorded on a scale comprising eight classes: 0, 1, 2, 4, 6, 8, 9, 10, ranging from completely unblemished to fully deceased plants. Because the procedure for evaluating foliage maturity type is less standardised, special care was taken in deciding which of the collected data to use for the final statistical analyses. In the year 2000, the variation between genotypes was highest when the first six successive assessments (August until mid-October)

were combined and adjusted for the length of the evaluation period (similar to relative AUDPC). Therefore, this combination of assessments was chosen for the statistical analyses in both years, and resulted in foliage maturity type values that ranged between 0 and 10, with low values for genotypes with late foliage maturity and high values for the ones with early foliage maturity.

#### *Data analysis*

All statistical analyses were performed with GenStat 6 (GenStat, 2002). Relative AUDPC and foliage maturity type values were analysed with the residual maximum likelihood (REML) method (Patterson & Thompson, 1971), because experiments were unbalanced (incomplete blocks) due to insufficient numbers of seed tubers of some genotypes. Genotype averages were estimated with the factors replicate (block) and genotype in the fixed part of the statistical model, and the factor replicate  $\times$  plot as random. Multiple-year averages were estimated with the factors year, year  $\times$  replicate, and genotype as fixed, and the factors year  $\times$  plot and year  $\times$  replicate  $\times$  plot as random. An additional analysis was performed in which relative AUDPC values were adjusted for foliage maturity type. This adjusted relative AUDPC was obtained by a two-step approach, the first analysis was done with the factors replicate and foliage maturity type in the fixed part of the statistical model. The resulting slope estimate for foliage maturity type was then used as offset in the subsequent analysis in which genotype averages were estimated with the factors replicate and genotype as fixed, and the factor replicate  $\times$  plot as random. Relative AUDPC values were not adjusted for foliage maturity type in the year 2001, because the absence of correlation between the two traits in this year (progeny 5) made such an adjustment pointless. Significances ( $P$  values) of the factors in the fixed part of the statistical analyses were obtained from the Wald statistics (chi-square distributed) as produced by the REML procedure, which also provided least significant difference values for pairwise comparisons ( $t$  test).

The phenotypic distributions for relative AUDPC and for foliage maturity type of each progeny were tested for skewness according to Sokal & Rohlf (1969). Transgression was significant when the value of any genotype of a progeny was significantly higher than the highest value of the two parents of that progeny, or when the value of any genotype was significantly lower than the lowest value of the two parents. To

determine whether differences between progeny genotypes and parents were significant, the least significant difference values from the REML procedure were used. The method of Owen (1962) was used to determine afterwards how many genotypes per progeny should have been tested to obtain reliable estimations of progeny means, with delta set at 10% of the observed range of variation for the trait.

Broad-sense heritabilities for relative AUDPC, foliage maturity type, and adjusted relative AUDPC were calculated using variance components that were estimated with REML, by dividing the respective genotype variance component by the respective sum of all variance components (Hanson, 1963). Variance components were estimated per progeny with the factor replicate in the fixed part of the analyses, and the factors genotype and replicate  $\times$  genotype as random. Variance components for progeny 5 (SH  $\times$  CE) for the combination of years were estimated with the factors year and year  $\times$  replicate as fixed, and the factors genotype, year  $\times$  genotype, and year  $\times$  replicate  $\times$  genotype as random.

Analyses of variance of progeny means for relative AUDPC, foliage maturity type, and adjusted relative AUDPC were based on experimental method 4 of Griffing (1956) for a half-diallel without parental selfings, and model I in which the parents are assumed to be fixed. The general and specific combining abilities (GCAs and SCAs) were estimated by multiple linear regression.

## Results

### *Foliage resistance to late blight*

Foliage resistance to late blight was evaluated in the field and all potato genotypes in both evaluations (2000 and 2001) developed symptoms of late blight. This absence of immune plants indicated that *R8* and *R9* were not effective in the tested material, because when these genes had been effective, they would have conferred absolute resistance against *P. infestans* (Turkensteen, 1989). Effects of the other nine known *R* genes were excluded by inoculation with a race of *P. infestans* that was virulent to these *R* genes (IPO82001, race 1.2.3.4.5.6.7.10.11).

Late blight resistance was expressed as relative Area Under the Disease Progress Curve (AUDPC), with low relative AUDPC values corresponding to resistance and high relative AUDPC values corresponding to susceptibility. The distributions for rel-

ative AUDPC (Figure 1) of progenies 1, 2, 3, 4, and 6 were significantly skewed towards resistance ( $P < 0.0005$ ). The distribution of progeny 5 was less skewed towards resistance in the year 2000 ( $P < 0.0025$ ) and not skewed at all in 2001. In the year 2000 all progenies showed transgression for relative AUDPC in both directions ( $P < 0.05$ ), whereas progeny 5 in 2001 only transgressed towards susceptibility ( $P < 0.05$ ). Relative AUDPC values for progeny 5 and all four parents were significantly lower in the 2nd year of testing ( $P < 0.05$ ; Figure 1, Table 3). This second evaluation in 2001 gave a better discrimination of the genotypes, as demonstrated by the larger differences between the parental values (Table 3), smaller LSD (Figure 1) and higher heritability (Table 4). Correlation ( $r$ ) between genotype means obtained in the 2 years of evaluation was 0.66.

The broad-sense heritability for resistance to late blight was estimated at 0.64 for all six progenies that were tested in the year 2000, but differences between progenies were apparent with a heritability as high as 0.80 for progeny 1 but only 0.49 for progeny 6 (Table 4). These differences between progenies reflected mainly differences in genetic variation ( $vc_g$ ). The broad-sense heritability for resistance against *P. infestans* of progeny 5 was different in the 2 years of evaluation and distinctly lower when the estimation was based on the combined analysis of both years (Table 4) due to genotype  $\times$  environment interactions.

The evaluation of late blight resistance that was performed in the year 2000 enabled a half-diallel analysis. The parental values for relative AUDPC were lowest for CE, highest for SH, and intermediate for DH and I (Table 3). The offspring of DH was on average as susceptible to late blight as its parent, as illustrated by the similar relative AUDPC values for the parent and the mean of the three progenies segregating from it (Table 3). The offspring of SH had on average lower relative AUDPC values than its parent, whereas the offspring of I and CE had on average higher relative AUDPC values than their respective parents. Parent CE had the best General Combining Ability (GCA) for resistance to late blight, reducing the mean relative AUDPC with 0.027 (Table 3). Parent I had the worst GCA, increasing the mean relative AUDPC with 0.032. As shown in Table 5, the parental combinations of progenies 3 and 4 resulted in the best specific combining abilities for resistance against *P. infestans* with an additional reduction of the relative AUDPC of 0.008. The parental combinations of progenies 1 and 6 gave

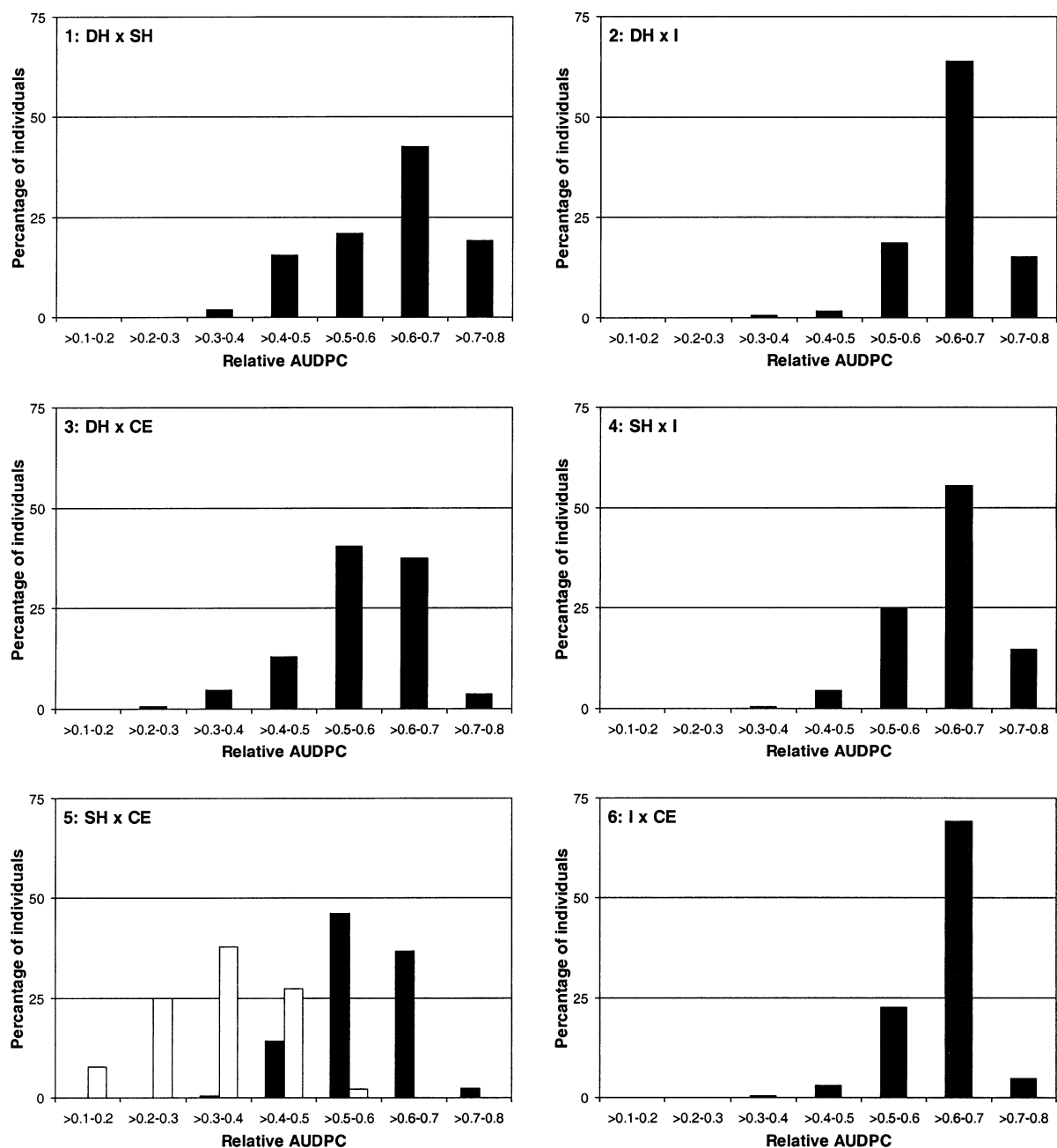


Figure 1. Relative frequency distributions of phenotypic classes of foliage resistance to late blight (relative AUDPC) for each of the six progenies (1 to 6) of the half-diallel set of crosses with the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE). Estimations based on field evaluations of the year 2000 (solid bars,  $LSD_{0.05}$ : 0.098) for all six progenies and additionally for progeny 5 in the year 2001 (open bars,  $LSD_{0.05}$ : 0.064).

the worst SCAs with an additional increase of 0.009 of the relative AUDPC. SCA effects were small compared to GCA effects. The GCAs for late blight resistance that were estimated in the year 2000 correlated poorly with the parental values of that year ( $r = 0.37$ ),

but correlated much better with the parental values of 2001 ( $r = 0.97$ ). As a consequence, the progeny means for resistance to late blight that were estimated in the year 2000 were more consistent with the midparent values of 2001 (not shown,  $r = 0.93$ ), than with the

Table 3. Late blight resistance (relative AUDPC), foliage maturity type, and late blight resistance adjusted for foliage maturity type (adjusted relative AUDPC) of the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE) of the half-diallel set of crosses. Parental values were obtained from evaluations in two successive years (2000 and 2001), adjusted relative AUDPC values were not determined in 2001. Offspring means and General Combining Abilities (GCAs) were obtained from the evaluation in the year 2000. Different letters within a column indicate significant differences ( $P = 0.05$ )

| Parent | Relative AUDPC                 |                                |                     | Foliage maturity type          |                                |                                |                     | Adjusted relative AUDPC        |                                |                                |                     |
|--------|--------------------------------|--------------------------------|---------------------|--------------------------------|--------------------------------|--------------------------------|---------------------|--------------------------------|--------------------------------|--------------------------------|---------------------|
|        | Parental Value <sub>2000</sub> | Offspring Mean <sub>2000</sub> | GCA <sub>2000</sub> | Parental Value <sub>2001</sub> | Parental Value <sub>2000</sub> | Offspring Mean <sub>2000</sub> | GCA <sub>2000</sub> | Parental Value <sub>2001</sub> | Parental Value <sub>2000</sub> | Offspring Mean <sub>2000</sub> | GCA <sub>2000</sub> |
| DH     | 0.61 ab                        | 0.61 b                         | -0.001 b            | 0.36 b                         | 4.6 a                          | 4.6 a                          | 0.44 a              | 3.0 a                          | 0.60 a                         | 0.60 a                         | -0.016 a            |
| SH     | 0.65 b                         | 0.60 b                         | -0.005 b            | 0.37 b                         | 4.4 a                          | 3.9 b                          | -0.27 b             | 3.0 a                          | 0.65 a                         | 0.62 a                         | 0.002 a             |
| I      | 0.60 ab                        | 0.64 c                         | 0.032 c             | 0.51 c                         | 4.2 a                          | 4.3 a                          | 0.21 a              | 2.8 a                          | 0.60 a                         | 0.64 b                         | 0.024 b             |
| CE     | 0.54 a                         | 0.58 a                         | -0.027 a            | 0.16 a                         | 1.8 b                          | 3.8 b                          | -0.37 b             | 1.6 b                          | 0.63 a                         | 0.61 a                         | -0.011 a            |

Table 4. Broad-sense heritabilities ( $h^2$ ) with genotype variance components ( $vc_g$ ) for late blight resistance (relative AUDPC), foliage maturity type, and late blight resistance adjusted for foliage maturity type (adjusted relative AUDPC) of the six progenies (1 to 6) of the half-diallel set of crosses with the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE), and the correlation ( $r$ ) between late blight resistance and foliage maturity type. Evaluations of all six progenies were done in the year 2000, and progeny 5 was tested again in 2001 where adjusted relative AUDPC values were not determined

| Progeny              | Cross   | Relative AUDPC |        | Foliage maturity type |        | $r$  | Adjusted relative AUDPC |        |
|----------------------|---------|----------------|--------|-----------------------|--------|------|-------------------------|--------|
|                      |         | $h^2$          | $vc_g$ | $h^2$                 | $vc_g$ |      | $h^2$                   | $vc_g$ |
| 1                    | DH × SH | 0.80           | 0.0084 | 0.70                  | 1.27   | 0.73 | 0.64                    | 0.0036 |
| 2                    | DH × I  | 0.66           | 0.0027 | 0.62                  | 0.66   | 0.56 | 0.52                    | 0.0015 |
| 3                    | DH × CE | 0.72           | 0.0061 | 0.44                  | 0.25   | 0.47 | 0.63                    | 0.0039 |
| 4                    | SH × I  | 0.56           | 0.0031 | 0.70                  | 1.01   | 0.51 | 0.43                    | 0.0019 |
| 5 <sub>2000</sub>    | SH × CE | 0.62           | 0.0037 | 0.44                  | 0.27   | 0.01 | 0.65                    | 0.0042 |
| 5 <sub>2001</sub>    | SH × CE | 0.84           | 0.0079 | 0.60                  | 0.16   | 0.18 | -                       | -      |
| 5 <sub>avg</sub>     | SH × CE | 0.56           | 0.0043 | 0.32                  | 0.13   | 0.13 | -                       | -      |
| 6                    | I × CE  | 0.49           | 0.0017 | 0.71                  | 0.64   | 0.48 | 0.39                    | 0.0011 |
| Mean <sub>2000</sub> |         | 0.64           |        | 0.60                  |        | 0.53 | 0.54                    |        |

mid-parent values of the year 2000 ( $r = 0.36$ ). With the standard deviation that was realised in the year 2000 progeny means for resistance against *P. infestans* could have been estimated accurately with a number of only 10 genotypes per progeny ( $\alpha = 0.05$ ,  $\beta = 0.10$ ; Owen, 1962). This indicates that progeny means were estimated very reliably in this study with progenies of 227 or 300 genotypes.

#### Foliage maturity type

Foliage maturity type was evaluated in the field, and six successive assessments were combined and adjusted for the length of the evaluation period resulting in values ranging between 0 and 10. Low values for foliage maturity type correspond to late foliage maturity and high values to early foliage maturity.

The progenies 1 and 4 showed a normal distribution for foliage maturity type (Figure 2), whereas the distribution of progeny 2 was significantly skewed towards early foliage maturity ( $P < 0.05$ ), and the distributions of progenies 3 and 6 were significantly skewed towards late foliage maturity ( $P < 0.0005$ ). The distribution of progeny 5 was significantly skewed towards early foliage maturity in the year 2000 ( $P < 0.0005$ ), whereas it was not skewed in 2001. Progenies 1, 2, and 4 transgressed for foliage maturity type in both directions ( $P < 0.05$ ), while progenies 3, 5, and 6 only displayed transgression towards early foliage maturity ( $P < 0.05$ ). Progeny 5 and all four parents had significantly lower values for foliage maturity type in the 2nd year of testing ( $P < 0.05$ ; Figure 2, Table 3). This second evaluation in 2001 enabled better discrimination of the genotypes, as indicated by the smaller

Table 5. Late blight resistance (relative AUDPC), foliage maturity type, and late blight resistance adjusted for foliage maturity type (adjusted relative AUDPC) of the six progenies (1 to 6) of the half-diallel set of crosses with the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE). Evaluations of all six progenies were done in the year 2000, resulting in mid-parent values, progeny means, and Specific Combining Abilities (SCAs). Different letters within a column indicate significant differences ( $P = 0.05$ ). Progeny 5 was tested again in 2001, where adjusted relative AUDPC values were not determined and SCAs could not be estimated

| Progeny              | Cross   | Relative AUDPC   |              |        | Foliage maturity type |              |       | Adjusted relative AUDPC |              |        |
|----------------------|---------|------------------|--------------|--------|-----------------------|--------------|-------|-------------------------|--------------|--------|
|                      |         | Mid-parent value | Progeny mean | SCA    | Mid-parent value      | Progeny mean | SCA   | Mid-parent value        | Progeny mean | SCA    |
| 1                    | DH × SH | 0.63             | 0.61 b       | 0.009  | 4.5                   | 4.4 ab       | 0.10  | 0.62                    | 0.61 b       | 0.005  |
| 2                    | DH × I  | 0.60             | 0.64 b       | -0.001 | 4.4                   | 4.6 a        | -0.16 | 0.60                    | 0.63 bc      | 0.004  |
| 3                    | DH × CE | 0.57             | 0.57 a       | -0.008 | 3.2                   | 4.3 ab       | 0.06  | 0.61                    | 0.58 a       | -0.009 |
| 4                    | SH × I  | 0.62             | 0.63 b       | -0.008 | 4.3                   | 4.1 b        | 0.06  | 0.62                    | 0.64 c       | -0.009 |
| 5 <sub>2000</sub>    | SH × CE | 0.60             | 0.58 a       | -0.001 | 3.1                   | 3.3 c        | -0.16 | 0.64                    | 0.62 bc      | 0.004  |
| 5 <sub>2001</sub>    | SH × CE | 0.27             | 0.34         | -      | 2.3                   | 2.6          | -     | -                       | -            | -      |
| 5 <sub>avg</sub>     | SH × CE | 0.43             | 0.46         | -      | 2.7                   | 3.0          | -     | -                       | -            | -      |
| 6                    | I × CE  | 0.57             | 0.62 b       | 0.009  | 3.0                   | 4.1 b        | 0.10  | 0.62                    | 0.64 c       | 0.005  |
| Mean <sub>2000</sub> |         |                  | 0.61         |        |                       | 4.2          |       |                         | 0.62         |        |

LSD (Figure 2) and higher heritability (Table 4). Correlation ( $r$ ) between genotype means obtained in the 2 years of evaluation was 0.40. To check whether this rather poor correlation was due to different temperature conditions in these years, the calculated foliage maturity type was adjusted not only for the time of evaluation, but also for the thermal time of evaluation. This adjustment for thermal time did not change the results for foliage maturity type notably, nor improve the correlation between the 2 years of evaluation (data not shown).

The broad-sense heritability for foliage maturity type was estimated as 0.60 for all six progenies that were tested in the year 2000, with heritabilities for individual progenies ranging from 0.44 for progenies 3 and 5, to 0.71 for progeny 6 (Table 4). Differences between progenies reflected mainly differences in genetic variation ( $vc_g$ ). The broad-sense heritability for foliage maturity type of progeny 5 was different in the 2 years of evaluation and rather low when the estimation was based on the combined analysis of both years (Table 4) due to genotype × environment interactions.

A half-diallel analysis was based on the evaluation of foliage maturity type of the year 2000. The parental values for foliage maturity type were lowest for CE and similarly high for DH, SH, and I (Table 3). The foliage maturity type of the offspring of DH was on average similar to that of its parent, as illus-

trated by the similar foliage maturity type values for the parent and the mean of the three progenies segregating from it (Table 3). The offspring of SH had on average lower foliage maturity type values than its parent, where the offspring of I and CE had on average higher foliage maturity type values than their respective parents. Parent DH had the most positive GCA for foliage maturity type, increasing the mean with 0.44 (Table 3). Parent CE had the most negative GCA, reducing the mean with 0.37. The parental combinations of progenies 1 and 6 showed the most positive SCAs for foliage maturity type with an additional increase of 0.10 (Table 5). The parental combinations of progenies 2 and 5 resulted in the most negative SCAs with an additional reduction of 0.16. SCA effects were small compared to GCA effects. The GCAs for foliage maturity type that were estimated in the year 2000 correlated moderately with the parental values of the years 2000 ( $r = 0.67$ ) and 2001 ( $r = 0.65$ ). Accordingly, the progeny means for foliage maturity type that were estimated in the year 2000 correlated also moderately with the midparent values of the years 2000 ( $r = 0.64$ ) and 2001 (not shown,  $r = 0.62$ ). With the standard deviation that was realised in the year 2000 progeny means for foliage maturity type could have been estimated accurately with a number of 13 genotypes per progeny ( $\alpha = 0.05$ ,  $\beta = 0.10$ ; Owen, 1962), indicating that progeny means were estimated very reliably in this study.

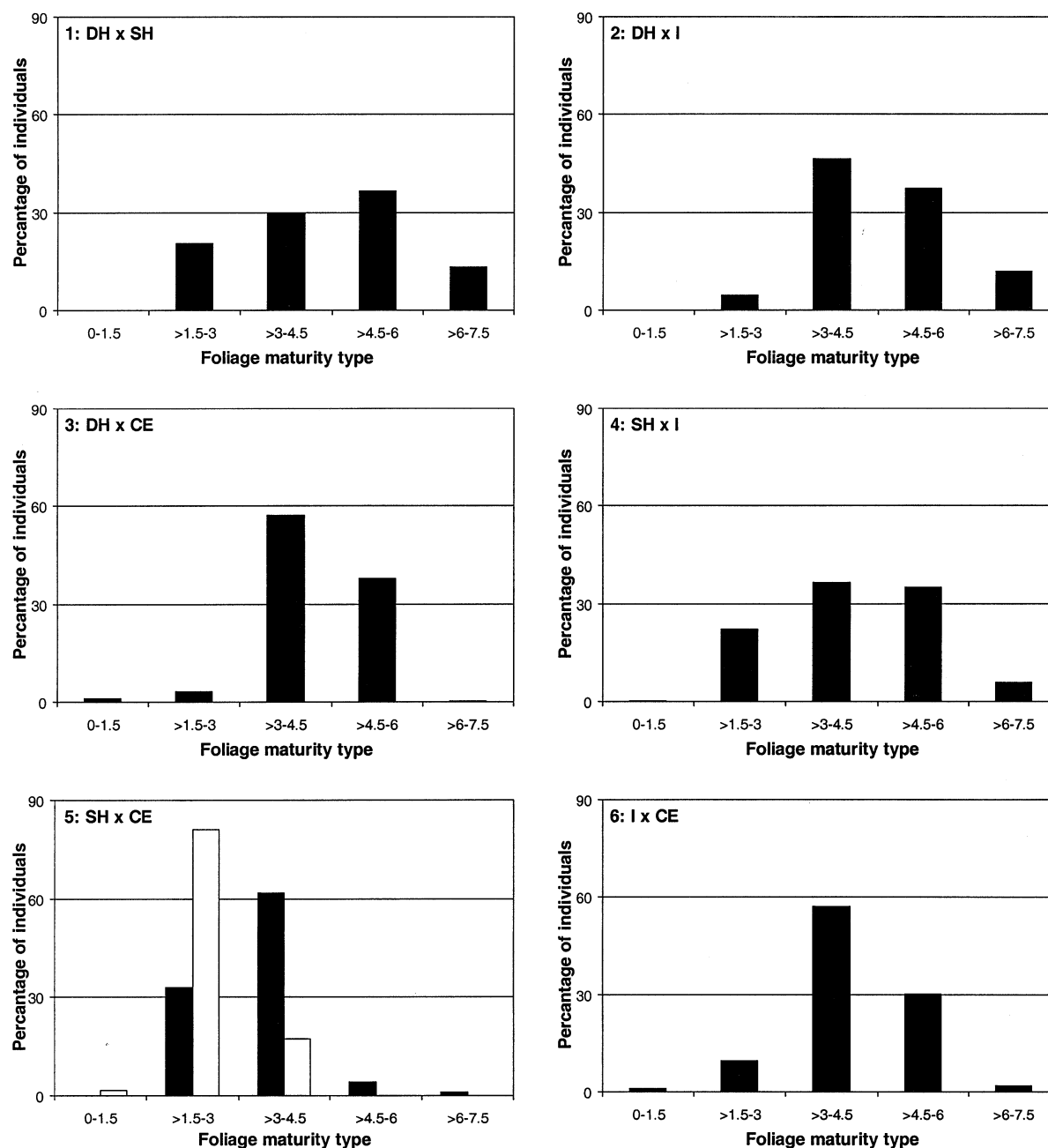


Figure 2. Relative frequency distributions of phenotypic classes of foliage maturity type for each of the six progenies (1 to 6) of the half-diallel set of crosses with the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I), and CE51 (CE). Estimations based on field evaluations of the year 2000 (solid bars,  $LSD_{0.05}$ : 1.33) for all six progenies and additionally for progeny 5 in the year 2001 (open bars,  $LSD_{0.05}$ : 0.54).

*Correlation between foliage resistance to late blight and foliage maturity type*

Progenies 1, 2, and 4 displayed a positive correlation ( $r$ ) between relative AUDPC and foliage maturity type:

low relative AUDPC values coincided with low values for foliage maturity type and high relative AUDPC values coincided with high values for foliage maturity type (Figure 3, Table 4). Progenies 1, 2, and 4 showed continuous variation of both relative AUDPC and foliage

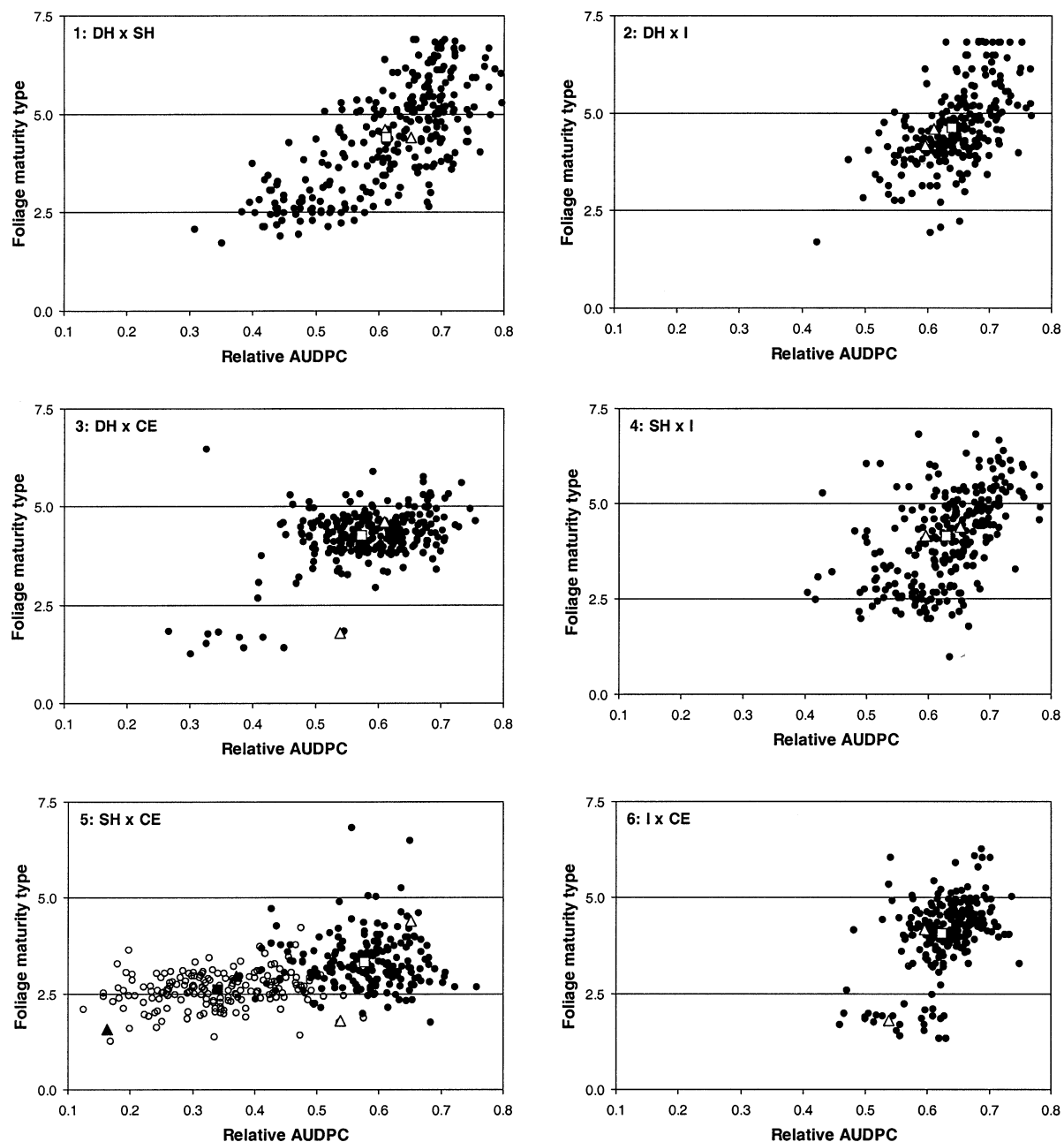


Figure 3. Correlation between late blight resistance (relative AUDPC) and foliage maturity type for each of the six progenies (1 to 6) of the half-diallel cross with the four diploid potato parents: DH84-19-1659 (DH), SH82-44-111 (SH), I88.55.6 (I) and CE51 (CE) based on field evaluations of the year 2000 (solid dots) for all six progenies and, additionally the year 2001 (open dots) for progeny 5. Parental values are indicated by triangles, progeny means by squares (open for 2000, solid for 2001).

maturity type (Figure 3). The variation of the two traits was different in progenies 3 and 6: there was a distinct, unequal separation into two classes of foliage maturity type with correlating relative AUDPC values. In both progenies a small group of genotypes had foliage

maturity type values of about 1.6 to 1.9 that were similar to one parent (CE), whereas a large group had foliage maturity type values of about 4.3 to 4.4 that were similar to the other parent (DH or I). In neither group was a correlation between relative AUDPC and foliage

maturity type apparent. In progeny 5 there was no correlation between relative AUDPC and foliage maturity type either, because there was almost no variation for foliage maturity type present in this progeny.

The half-diallel analysis of relative AUDPC values that were adjusted for foliage maturity type was based on the evaluations of the two traits in the year 2000. The values of adjusted relative AUDPC were similar for all four parents (Table 3). The offspring of SH and CE had on average lower adjusted relative AUDPC values than their respective parents, whereas the offspring of DH and I had on average higher adjusted relative AUDPC values than their respective parents (Table 3). Parent DH had the best GCA for adjusted relative AUDPC, reducing the mean with 0.016 (Table 3). Parent I had the worst GCA, increasing the mean with 0.024. The parental combinations of progenies 3 and 4 resulted in the best SCAs for adjusted relative AUDPC with an additional reduction of 0.009 (Table 5). The parental combinations of progenies 1 and 6 gave the worst SCAs with an additional increase of 0.005. SCA effects were small compared to GCA effects.

Among all 1727 genotypes tested, there was only one positive recombinant with a low value for relative AUDPC and a high value for foliage maturity type. Attempts to confirm the phenotype of this genotype of progeny 3 were not successful.

## Discussion

The association between race-non-specific foliage resistance against *P. infestans* and foliage maturity type in potato was studied with six progenies that were derived from crosses between four unrelated diploid parents. The progenies were evaluated for resistance to late blight and for foliage maturity type, and five of them showed a significant correlation between the two traits. No correlation was found in progeny 5 due to the lack of variation for foliage maturity type. The correlation between late blight resistance and foliage maturity type varied between progenies, with similar patterns for progenies 1, 2, and 4, and similar patterns for progenies 3 and 6. Despite its significance, the correlation did not account for all variation that was present for the two traits: different genotypes with similar values for foliage maturity type still extended over quite a range of relative AUDPC values in all progenies (Figure 3).

This remaining variation for resistance against *P. infestans* was reflected in the analysis in which the relative AUDPC values were adjusted for foliage maturity type. The variation between general combining

abilities (GCAs) was reduced with about 30%, but differences were still significant. The  $vc_g$  values for adjusted relative AUDPC also indicate that there is genetic variation for late blight resistance that is independent of foliage maturity type. Despite a considerable reduction in  $vc_g$  values for most progenies (~50%), broad-sense heritabilities were reduced only slightly and were still high enough to expect a reasonable response to selection.

The transgression of the phenotypic distributions for resistance to late blight suggests effects of multiple alleles and/or loci: different alleles and/or loci from the different parents have combined into more extreme genotypes in the offspring. The correlation between late blight resistance and foliage maturity type indicates that at least one locus for resistance must be linked with a locus for foliage maturity type. This is supported by QTLs for both traits that were identified on chromosome 5 of parents I and CE in previous crosses: the allele that conferred resistance against *P. infestans* also conferred late foliage maturity (Collins et al., 1999; Oberhagemann et al., 1999; Visker et al., 2003). The remaining variation for resistance to late blight after adjustment for foliage maturity type indicates that not all loci for resistance are linked with loci for foliage maturity type. This corresponds with QTLs for late blight resistance that are not linked with QTLs for foliage maturity type, like QTLs on several chromosomes in parent I (Collins et al., 1999; Oberhagemann et al., 1999), and a QTL on chromosome 3 in parent CE (Visker et al., 2003).

Separate evaluations and subsequent analyses of resistance to late blight and of foliage maturity type were performed in order to investigate the correlation between the two traits and to enable the adjustment of relative AUDPC values for foliage maturity type.

For the phenotypic evaluations of race-non-specific resistance against *P. infestans*, precautions were taken to ensure that the observed resistance was not caused by any of the 11 known *R* genes. It was verified whether the detected skewness was due to the method of evaluation, because this is quite possible in assessments in which all objects eventually reach disease ratings of 100%. However, similar skewness was found when only 4 instead of 6 weeks of observations were included in the calculation of relative AUDPC values, which demonstrates that the skewness did not result from a period of evaluation that was too long. In addition, variance-stabilising data transformation was considered for all results, but proved to be unnecessary because residuals did not depend on fitted values. The

correlation between parental values and GCAs for late blight resistance (Stewart et al., 1992; Bradshaw et al., 1995) indicates that phenotypic values of the parents can be used as reliable estimates of breeding values (Bradshaw et al., 1995), provided that effects of genotype  $\times$  environment interactions are minimised by using multiple-year averages. The resulting midparent values then provide satisfactory predictions of the mean progeny performances (Neele et al., 1991). The good GCA of CE suggests that this parent should be used to improve resistance to late blight.

The phenotypic evaluations of foliage maturity type resulted in values that were based on a combination of the first six successive assessments. Statistical analyses were also performed for each separate assessment of the year 2000, and the results of assessments 1, 2, and 3 were very similar to one another and to the results of the combination of six assessments. Thus, assessing foliage maturity type just once a season (Oberhagemann et al., 1999; Van Eck, 1995; Visker et al., 2003) can be as informative as evaluating over a period of several months, as long as the moment of assessment is chosen properly (within a month after the first signs of senescence become visible). The moderate correlation between parental values and GCAs for foliage maturity type (Bradshaw et al., 2000) indicates that the phenotypic values of the parents cannot be used for the estimation of breeding values. This moderate correlation is due to Specific Combining Ability (SCA) effects. The variation for foliage maturity type of progenies 3, 5, and 6 suggest that these SCA effects are caused by non-additive properties (dominance, epistasis) of parent CE, or result from distorted segregation in progenies 3 and 6. When SCA effects are relevant, testcrosses, like a diallel, can be a valuable alternative to determine breeding values (Neele et al., 1991). The most positive GCA of DH indicates that this parent should be used to obtain early foliage maturity.

Parent DH is the most promising of this half-diallel, because the most positive GCA for foliage maturity type was not accompanied by a poor GCA for late blight resistance, which resulted in the best GCA for adjusted relative AUDPC. However, even the offspring of this most favourable parent (progenies 1, 2, and 3) did not contain the desired genotypes in which resistance to late blight was combined with early foliage maturity.

The present study confirms the results of Toxopeus (1958): resistance against *P. infestans* always coincides with late foliage maturity. This correlation is similar to that in commercial, tetraploid potato varieties (Swiezynski, 1990; Anonymous, 2003), despite

the contrast that varieties have been selected for many commercially important traits and the progenies of the half-diallel were evaluated without prior selection. However, the present study also indicates that some selection for resistance to late blight without affecting foliage maturity type should be possible, probably due to the presence of QTLs for resistance that are not linked with QTLs for foliage maturity type.

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