Theor Appl Genet (1991) 82:264–272

Identification of superior parents in a potato breeding programme

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Received July 23, 1990; Accepted January 23, 1991
Communicated by A. R. Hallauer

Summary. An incomplete diallel cross was used to study components of genetic variation in potatoes for a range of characters after early and late harvest. The progenies were also used to evaluate five predictors of progeny performance, namely the mean seedling performance, the mid-parent value and the means of the selfed progenies, of the diploid progenies and of the test-cross progenies. For almost all characters, the general combining ability effects were predominant, although the specific combining ability effects present were greater at late than at early harvests. The seedling performance for tuber yield, number of tubers and average tuber weight did not show any relevant relationship to the field performance. The mid-parent value provided, in general, satisfactory predictions of the mean progeny performance obtained in the diallel, except for ware tuber yield. The selfed and the diploid progenies did not improve the prediction of progeny means compared to the mid-parent value. The predictions based on the test-crosses surpassed those of the mid-parent value, particularly for tuber yield at ware potato harvest. Methods to identify superior parents are discussed.

Key words: Potato – *Solanum tuberosum* L. – Parental choice – GCA – SCA – Combining ability – Mid-parent value – Selfing – Diploids – 4x-2x Test-crosses – Inheritance

Introduction

The selection of superior parental combinations to a large extent determines the degree of success of a potato breeding programme. The proper evaluation of clones as suitable parents is therefore crucial for breeders, and several adequate methods, such as diallel crosses (Griffing 1956) and the North Carolina Design II (Comstock and Robinson 1952), have been described as being useful in this evaluation. In practical breeding, however, these are rarely used due to the considerable amount of time and labour required for these designs and the difficulty in obtaining the crosses necessary. Other less costly methods of predicting progeny performance are therefore required in order to improve the choice of parents and thus the efficiency of a breeding programme.

The most simple method for predicting the value of cross combinations is to evaluate progenies at seedling stage. If a close relation between seedling performance and performance in subsequent field generations exists, as found by Brown and Caligari (1989) for tuber yield and plant appearance and by Neele and Louwes (1989) for chip quality and dry-matter content, progeny selection could be carried out at the seedling stage.

An alternative approach for the North Carolina Design II might be test-crosses with desynaptic diploid 2n-FDR-pollen producing male parents. Since these genotypes produce genetically homogeneous pollen (Iwanaga 1984), only small test-progenies would be needed to evaluate the breeding value of the female parents.

Diploids derived directly from a tetraploid clone by anther culture or by pollination with *S. phureja* (Hermsen and Verdenius 1973) might also be used to evaluate the parental value of a clone (Hougas and Peloquin 1958). Since by this method unfertilized pollen- or egg cells develop into plants, a glimpse is offered into the genetic background of potential parents. Matsubayashi (1979) used this method to survey segregation for morphological characters in the diploid progeny of cv 'Chippewa' and Maris (1973) used diploid offspring to study the

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inheritance of resistance to wart disease (*Synchytrium endobioticum*). For each parental clone only one progeny family needs to be assessed. This method, however, demands significant effort to obtain enough diploids. In earlier research we reported that by pollinating with *S. phureja* we required 3 months of labour and 300 m^2 of glasshouse area to obtain 10,000 diploid seeds from 22 varieties, while only about 50% of these seeds could be used for further evaluation. The other seeds did not germinate, died soon after germination or showed severe growth abnormalities (Neele and Louwes 1986). Caligari et al. (1988) similarly reported a germination percentage of only 61%, and again only 61% of these were viable diploids.

Another method by which to predict the breeding value might be selfing. This method has the additional advantage that it requires only one offspring population per evaluated parent, but it can only be applied to male-fertile parental clones. Feistritzer (1952) used selfed progenies to predict breeding value, but the data did not provide acceptable predictions for hybridization programmes and only described the rate of homozygosity of the parents. Brown and Caligari (1989) found moderate correlation coefficients between the 'mid-self value' (in analogy to the mid-parent value) and the actual mean value of a progeny for plant appearance, mean tuber weight and number of tubers. For total tuber weight the correlation was even better.

The most widely used predictive method is the mid-parent value. Maris (1989) obtained moderate to good correlation coefficients ($r=0.51$ to $r=0.85$) between the mid-parent value and the actual progeny performance for various agronomically important characters. For yield and number of tubers, however, the correlations were relatively poor ($r=0.51$ and $r=0.59$ respectively). Brown and Caligari (1989) were not able to accurately predict the progeny performance by the mid-parent value. This suggests that a prediction based on the mean of the parental values might have limited value and migth not result in progenies with the best prospects.

In this paper the genetic and economic advantages and drawbacks of five methods for predicting the performance of cross combinations are compared: the seedlings, the mid-parent value, diploid progenies, selfed progenies and test-cross progenies obtained with diploid 2n-FDR pollen producing males.

Materials and methods

Genotypes

Six tetraploid clones, the varieties 'Alcmaria,' 'Désirée,' 'Maritta' and 'Pimpernel,' and the breeding lines AM74-602 and MPI49-540/2 were used in a hybridization programme. These clones cover a wide range in agronomic performance and maturity. Furthermore, the clones are unrelated: the coefficient of parentage (I) (Kempthorne 1957) for the progeny of 'Alcmaria' × 'Désirée' was $I=0.016$; for the progeny of Désirée × 'Pimpernel,' $I=0.008$; for the other progenies, $I=0$. Since the parental clones used reflect a wide range in performance, maturity and genetic background, which is the common situation in potato breeding, the results obtained in this study may be indicative for breeding programmes in general.

The clones were crossed in 1983 and 1984 in a incomplete diallel (diallel), resulting in 20 progenies. Each parent was represented in 6 or 7 progenies, equally as male and as female parent.

Diploid progenies were produced after pollination with *Solanum phureja* IVP35 and IVP48 (Hermsen and Verdenius 1973). Six diploid males producing 2n-FDR-pollen, M6, SY7, BE-62, CE-10, FB-107 and Phu75-1136-1936-680 (P680), were used for the test-crosses. The first four are desynaptic and the last two synaptic.

Experiments

The seedling generations were grown in 11 × 11-cm pots during the spring and summer of 1984 (diallel) and 1985 (diploids, selfed progenies and test-crosses) under glasshouse conditions in Wageningen. All successive trials were performed on a clay soil in the Dutch New Polders on an experimental farm near Lelystad. The plant distance was 35 cm within and 75 cm between the ridges.

It was not possible to perform all of the experiments during the same time period since the labour requirements were to high. Therefore, the experiments were spread out over time. The mid-parent value predictor was evaluated in 1986 and 1987; the diploid progenies were grown in 1986 (early harvest only), 1988 and 1989; the selfed progenies in 1987–1989; the test-crosses in 1986 (early harvest only), 1987 and 1988. The diallel was evaluated from 1986 to 1989.

In all of the trials progenies were the main experimental unit and 30 clones per progeny, taken at random, were randomized within these plots with two plants per clone. The experiments were performed in two replications. To reduce the labour inputs of the diallel experiments in 1988 and 1989, the clones within each progeny of the diallel were not distinguished individually, and the progenies were evaluated as a single experimental unit. In each progeny unit, clones were represented by one plant, and to maintain the number of plants tested per progeny, the latter experiments were performed in four replications. In 1986 and 1987, the parental clones of the diallel were randomized among their offspring in order to calculate the mid-parent value. Two harvests were carried out each growth season: in mid-July, to harvest virus-free seed potatoes, and in mid-September, for the mature crop evaluation.

The experiments of the diallel, test-crosses, selfed progenies and diploid progenies were carried out and analysed as separate experiments. The experimental design of all trials was a complete randomized block design.

Characters measured

Every seedling of the diallel was assessed for tuber weight and number of tubers after growth in the glasshouse in 1984. Subsequently, the mean tuber weight was calculated. During the growing season, the field experiments were evaluated for early season growth (1 = slow growth, 9 = rapid growth) and for number of stems in mid-June. At harvest, plant appearance (1 = poor, 9 = excellent) was assessed; at the seed potato harvest, stolon length (1 = long, 9 = short) and fresh weight of the foliage (g). Afterwards, tuber yield (g) and the number of tubers over and under 30 mm ∅ were determined. In addition, visual assessments were made of skin colour (1 = yellow, 4 = purple), tuber shape (1 = round, 5 = long), regularity of tuber shape (1 = irregular, 9 = regular) and eye depth (1 = deep eyes, 9 = shallow). At

Table 1. Model for the analysis of variance of the general and specific combining ability effects (GCA and SCA) and the reciprocal effects (RE)

Source	*df*	Expected mean squares
GCA	5	$5.3\sigma^2_{gca} + 1.43\sigma^2_{sca} + 3.10\sigma^2_{re} + \sigma^2_e$
SCA	9	$1.26\sigma^2_{sca} + 0.86\sigma^2_{re} + \sigma^2_e$
RE	5	$0.79\sigma^2_{sca} + 3.55\sigma^2_{re} + \sigma^2_e$
Error[a]	38	σ^2_e

[a] The error variance is calculated from the analysis of variance of the 1986 and 1987 trials based on the progeny means

ware potato harvests also, the underwater weight (in g/5 kg tubers) was determined. Subsequently, the following characters were calculated: average tuber weight, the proportion of the total tuber weight accounted for by tubers under 30 mm, total biomass (=tuber yield+foliage yield) in July (g), and harvest index (=tuber yield/total biomass) in July.

Analysis

The 20 progenies were used to estimate the general and specific combining ability (GCA and SCA) effects. For all characters the GCA, SCA and Reciprocal Effects (RE) were analysed following Keuls and Garretsen (1977) for the random model (Table 1).

The analyses performed were based on the progeny means as well as on the within-progeny variance. The latter calculations were performed to examine whether differences between within-progeny variances could be attributed to certain parents or to specific combinations. If differences in the within-progeny variances strongly depend on specific combining ability, breeders can focus on the prediction of the progeny mean. On the other hand, if certain parents contribute to the within-progeny variation more than others, this should also be evaluted in order to obtain a proper prediction of the success of a progeny. In such cases, estimates of the mean and the within-progeny standard deviation should be calculated for the prediction of the chance that superior clones can be obtained in a hybrid population.

Since the variance estimates of normally distributed characters are themselves not normally distributed but chi-square distributed, a logarithmic transformation (ln) was performed on the within-progeny variances in order to carry out an analysis of variance.

The predictive value of the seedling performance and the four alternative predictors was evaluated using correlation coefficients. For each of the predictive methods, the mean performance of the parents was calculated; for the selfed and the diploid progenies, the progeny mean was calculated; and for the test-crosses, the mean performance of a maternal clone was avaraged across the male testers. Subsequently, these values were combined following the scheme of the diallel, and this predictor was correlated to the actual values obtained in the diallel. In equations:

Predictor for cross $P_i \times P_j$	Equation
Mean of diploid progeny (D_i)	$0.5\ (D_i+D_j)$
Mean of selfed progeny (S_i)	$0.5\ (S_i+S_j)$
Mean of test-cross progenies ($P_i \times$ (male testers)) (TC_i)	$0.5\ (TC_i+TC_j)$
Mid-parent value	$0.5\ (P_i+P_j)$

Subsequently, the predictor was averaged over all experimental years and correlated with the progeny mean results from the diallel over the years 1986–1989.

Results and discussion

Analysis of the incomplete diallel

The GCA variance was the most important source of variation at the early and late harvest for all characters (Table 2) except proportion of weight contributed by tubers under 30 mm at early harvest. At late harvest the differences between the GCA and SCA variance of tuber yield and the proportion of weight contributed by tubers under 30 mm were not large. If the prediction of the performance of hybrid populations in mainly based on the correlation with the parental GCAs, the possibilities of predictions seems to be promising, except for ware tuber yield and the contribution of tubers under 30 mm. Tai (1976) calculated a higher proportion of the total genetic variance accounted for by the SCA variance than in this study; the tendency, however, was similar. Tai found that the variation between progenies for tuber yield and number of tubers was dominated by the SCA variance, and for average tuber weight and specific gravity, the contribution of the GCA variance was most significant. Maris (1989) found, like in this study, predominating GCA variances for most characters, with the exception of yield, where the RE-variance was largest. Brown and Caligari (1989) described a predominant GCA effect for total tuber yield, number of tubers and plant appearance, and the mean tuber weight to be dependent on GCA and SCA effects. Killick (1977) found SCA to be most significant for many characters of agricultural importance. Killick, however, probably used more related parents, since all originated from the Scottish Crop Research Institute, in contrast to the genotypes used in our study and those of Tai (1976), Maris (1989) and Brown and Caligari (1989). In related material the number of different alleles is likely to be limited. Consequently, variation in additive gene action is limited as well, whereas non-additive gene action, like epistasis, can result in a relatively large between-progeny variation. In such experiments the SCA effects are likely to be prominent.

The GCA-within-progeny variance clearly exceeded the SCA and RE within-progeny variance only for the characters stolon length, number of tubers, weight proportion of tuber under 30 mm, average tuber weight and harvest index (Table 3). Parents with short stolons like 'Alcmaria' and MP149-540/2 contributed less to the within-progeny variance than parents with long stolons, ('Pimpernel'). The progenies of 'Alcmaria' also showed less variation for proportion of tubers under 30 mm, and for harvest index. The progenies of 'Désirée' and 'Alcmaria' showed lower variation for average tuber weight at early as well as at late harvest. Clones with early tuber formation like 'Alcmaria' and Désirêee' have been found to shift toward early tuberizing clones in their offspring (Neele 1990). In early tuberizing progenies, a small pro-

Table 2. GCA, SCA and RE variances estimated from the diallel of 1986 and 1987

	Seed potato harvest				Ware potato harvest			
	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}
Early season growth	0.172	0.020	0.018	0.0108	–	–	–	–
Number of stems	0.519	0	0.154	0.126	–	–	–	–
Stolon length	1.218	0.146	0	0.030	–	–	–	–
Plant appearance	0.881	0.105	0	0.025	0.271	0.091	0	0.024
Skin colour	0.200	0.047	0	0.001	0.237	0.052	0	0.001
Tuber shape	0.194	0.050	0	0.004	0.127	0.053	0	0.003
Regularity tuber shape	0.230	0.098	0	0.038	0.342	0.086	0	0.012
Eye depth	0.910	0.152	0	0.036	1.178	0.223	0	0.025
Tuber yield	68,185	4,337	0	513	34,752	29,981	5,909	2,707
Number of tubers	16.34	3.15	1.30	0.79	13.49	5.46	0	0.96
Prop. weight by tubers <30 mm	0	21.5	8.0	0.84	0.686	0.553	0.161	0.086
Number of tubers per stem	0.164	0.073	0.004	0.038	–	–	–	–
Average tuber weight	55.0	7.8	0	1.2	75.6	29.5	4.7	2.6
Foliage weight	3,015	932	890	1,497	–	–	–	–
Harvest index	56.2	6.1	0	0.6	–	–	–	–
Total biomass	49,353	8,037	0	2,584	–	–	–	–
Underwater weight	–	–	–	–	808.0	109.9	0	9.9

–, Means not measured
Those variances estimated negative were set to 0

Table 3. Estimated GCA, SCA and RE variances, obtained from the (logarithmically transformed) within-progeny variance of the diallel progenies

	Seed potato harvest				Ware potato harvest			
	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}
Early season growth	0.0408	0.0424	0	0.0232	–	–	–	–
Number of stems	0.0059	0.0088	0	0.0324	–	–	–	–
Stolon length	0.0874	0.0451	0	0.0310	–	–	–	–
Plant appearance	0.0195	0.0147	0.0055	0.0114	0.0220	0.0234	0.0135	0.0094
Tuber shape	0.0300	0.0500	0.0170	0.0175	0	0.0120	0	0.0104
Regularity tuber shape	0.0073	0.0419	0.0059	0.0147	0.0546	0.0589	0	0.0133
Eye depth	0.0195	0.0293	0	0.0151	0.0515	0.1051	0	0.0174
Tuber yield	0.0024	0.0402	0	0.0088	0.0322	0.0283	0.0020	0.0087
Number of tuber	0.0817	0.0204	0	0.0146	0.0771	0.0378	0.0006	0.0146
Prop. weight by tubers <30 mm	0.4103	0.0906	0.0681	0.0189	0.1167	0.3862	0	0.0997
Number of tubers per stem	0.0568	0.0746	0	0.0617	–	–	–	–
Average tuber weight	0.1649	0.0638	0	0.0193	0.0853	0.0375	0.0070	0.0203
Foliage weight	0	0.0108	0.0013	0.0119	–	–	–	–
Biomass	0	0.0330	0	0.0115	–	–	–	–
Harvest index	0.0314	0.0079	0.0173	0.0104	–	–	–	–
Underwater weight	–	–	–	–	0.0001	0.0375	0.0009	0.0092

–, Means not measured

portion of the clones had small tubers, expressed in the proportion of tubers under 30 mm, or a low harvest index, resulting in a significant GCA within-progeny variance. This shows that for most characters the within-progeny variance mainly depends on the parental combination and is therefore not predictable, while for some characters it could be attributed to the time of tuberization. This suggests that parental effects on within-progeny variances are likely to be combination dependent and need not be taken into account for the evaluation of prediction methods.

Evaluation of the predictive methods

Mean seedling performance. After harvest, the tubers of the seedlings of the diallel were weighed and counted. The correlation coefficients between the seedling progenies and the ware potato harvest performances in the subsequent years varied between $r=-0.36$ and $r=0.07$ for total tuber yield, between $r=-0.08$ and $r=0.14$ for number of tubers and between $r=-0.26$ and $r=-0.19$ for mean tuber weight. These poor correlation coefficients show that seedling progeny performance is not likely to be a good measure of field performance. Maris (1988) also observed poor relationships between glasshouse seedlings and field performance for number of tubers and average tuber weight, while the correlation for tuber yield was moderate ($r=0.44$ to 0.52). In contrast, Brown and Caligari (1989), using the progeny mean added to the within-progeny standard deviation, found a high correlation coefficient for tuber yield ($r=0.90$), moderate for mean tuber weight ($r=0.46$) and poor for number of tubers ($r=0.11$). A similar approach, however, did not improve the low correlation coefficients found in our study. Because the correlation between the seedling performance and these three important characters was extremely poor, no further analyses using seedling performance were carried out.

Mid-parent value. The seed potato harvest prediction by the mid-parent value was found to be very good for most characters, with many correlation coefficients exceeding $r=0.8$ (Table 4). Moderate correlation coefficients were noted for foliage weight, number of stems, tuber shape and number of tubers. At ware potato harvest, the correlation coefficients were lower, tuber, yield in particular was poorly predicted by the mid-parent value. In general, the correlation coefficients of the results averaged over years were better than the mean of the coefficients of 1986 and 1987. Hence, when the mean performances over years is used for calculating the correlation coefficients, a slight over-estimation with respect to correlation in 1 year is likely to occur. These results are similar to those obtained by Maris (1989) and Brown and Caligari (1989).

Diploids. The predictive value of the diploid progeny of a tetraploid clone for the breeding value of a clone was found to be limited (Table 5). Many correlation coefficients were equal to or lower than those obtained with the mid-parent value, and some were higher. At ware potato harvest the correlations were very poor except for underwater weight and skin colour, regularity of tuber shape and eye depth averaged over years. A possible reason for the poor value of this predictor is that in the diploid progenies many poorly growing plants occurred that seemed to be unrelated to the breeding value of the tetraploid parent. 'Désirée', for instance, had a large proportion of small, slowly developing plants, which was not the case in its tetraploid progenies. It is thought that after pollination with *S. phureja,* recessive deleterious alleles are present in a homozygous state. In a tetraploid most such recessive alleles will go unnoticed.

Selfed progenies. The seed potato harvest prediction by means of the selfed progenies was similar to those obtained with the mid-parent values (Table 5). Some traits were better predicted by the selfed progenies, like number of stems, tuber yield and total biomass, for some others

Table 4. Correlation coefficients of the progeny means of the incomplete diallel with the mean of the phenotypic value of parents ($df=18$)

	Seed potato harvest			Ware potato harvest		
	1986	1987	Mean	1986	1987	Mean
Early season growth	0.61	0.81	0.83	0.55	0.68	0.68
Number of stems	0.40	0.59	0.58	–	–	–
Stolon length	0.86	0.90	0.90	–	–	–
Plant appearance	0.88	0.84	0.89	0.73	0.55	0.64
Skin colour	0.90	0.89	0.90	0.89	0.87	0.89
Tuber shape	0.58	0.68	0.63	0.39	0.59	0.50
Regularity of tuber shape	0.86	0.77	0.87	0.85	0.79	0.85
Eye depth	0.83	0.84	0.85	0.84	0.72	0.78
Tuber yield	0.92	0.90	0.90	0.16	0.24	0.14
Number of tubers	0.32	0.77	0.55	0.38	0.59	0.57
Prop. weight by tubers <30 mm	0.81	0.87	0.87	0.63	0.72	0.73
Number of tubers per stem	0.79	0.79	0.86	–	–	–
Average tuber weight	0.89	0.92	0.86	0.72	0.76	0.81
Foliage weight (July)	0.32	0.48	0.54	–	–	–
Total biomass (July)	0.70	0.59	0.67	–	–	–
Harvest index (July)	0.86	0.92	0.89	–	–	–
Underwater weight	–	–	–	0.67	0.75	0.74

$P\ (r \geq 0.44) < 0.05$; $P\ (r \geq 0.56) < 0.01$
–, Means not measured

Table 5. Correlation coefficients of the progeny means of the incomplete diallel averaged over the years 1986–1989, with either the average of the means of the diploid progenies of the parents, those of the selfed progenies or those of the 4x-2x test-cross progenies ($df = 18$)

	Seed potato harvest				Ware potato harvest			
	Mid-parent	Diploid progeny	Selfed progeny	Test crosses	Mid-parent	Diploid progeny	Selfed progeny	Test crosses
Early season growth	0.83	0.22	0.91	0.57	0.68	0.20	0.74	0.74
Number of stems	0.58	0.54	0.74	0.75	–	–	–	–
Stolon length	0.90	0.55	0.89	0.94	–	–	–	–
Plant appearance	0.89	0.87	0.95	0.96	0.64	0.52	0.43	0.84
Skin colour	0.90	0.91	0.90	0.91	0.89	0.92	0.91	0.93
Tuber shape	0.63	0.75	0.81	0.91	0.50	0.63	0.46	0.80
Regularity of tuber shape	0.78	0.93	0.64	0.94	0.85	0.83	0.32	0.92
Eye depth	0.85	0.88	0.77	0.94	0.78	0.85	0.66	0.93
Tuber yield	0.90	0.82	0.96	0.93	0.14	−0.32	0.50	0.83
Number of tubers	0.55	0.53	0.36	0.69	0.57	0.58	0.85	0.74
Prop. weight by tubers <30 mm	0.87	0.88	0.51	0.87	0.73	0.50	0.75	0.47
Number of tubers per stem	0.86	−0.46	−0.42	0.37	–	–	–	–
Average tuber weight	0.86	0.88	0.86	0.87	0.81	0.51	0.82	0.70
Foliage weight (July)	0.54	0.29	0.58	0.70	–	–	–	–
Total biomass (July)	0.67	0.41	0.87	0.32	–	–	–	–
Harvest index (July)	0.89	0.79	0.91	0.93	–	–	–	–
Underwater weight	–	–	–	–	0.74	0.83	0.94	0.94

$P\ (r \geq 0.44) < 0.05$; $P\ (r \geq 0.56) < 0.01$
–, Means not measured

the prediction was inferior, like number of tubers, number of tubers per stem, and the proportion of the weight by tubers under 30 mm.

At ware potato harvest, the correlations proved to be inadequate for the prediction of most characters. Only for tuber yield, number of tubers, and underwater weight were the correlation coefficients higher than those obtained using the mid-parent value; a few were equal, like early season growth, skin colour, tuber shape, proportion of the weight by tubers under 30 mm and average tuber weight, or worse. Therefore, there is little or no advantage in using the mean of two selfed progenies as predictor for the ware potato harvest over the use of the mid-parent value.

4x-2x Test-crosses. Of the six testers used in these experiments two, CE-10 and FB-107, tuberized very late. A significant number of clones of the progenies of these clones with the late varieties 'Pimpernel' and 'Maritta' were unable to produce enough seed tubers in mid-July, and therefore all progenies with these males were eliminated. For application of the test-crosses in breeding only early tuberizing males should be used.

Both at seed and at ware potato harvest, the test-crosses provided good estimates for the actual values of the progenies (Table 5). For many characters the correlation coefficients exceeded $r = 0.8$ at seed potato harvest as well as at ware potato harvest.

For prediction at seed potato harvest the test-crosses were of at least equal value as the mid-parent value. Only early season growth, the number of tubers, the number of tubers per stem and total biomass were better predicted by the mid-parent value; prediction of the other characters by the test-crosses was equivalent or better. At ware potato harvest, the results of the test-cross predictions seemed to be superior to those of the mid-parent value, especially for tuber shape, tuber yield and underwater weight. The latter two characters are of prime importance in a commercial breeding programme, and test-crosses with diploid 2n-FDR pollen-producing males should be considered in preference to the mid-parent value.

In breeding practice the prediction of progeny performance is generally based on experiments that are carried out in different years than those when the actual progenies are tested. Genotype-year interactions are likely to influence the results of Table 5, and the merits of predictions from one year to another are important. In Table 6 predictions of f.i. ware potato tuber yield are related with the actual ones in different years (Table 6); year interactions are seen to be present, but its influence is of minor importance only. For the other traits similar results were obtained. In addition, such a procedure indicates that test-crosses are the most promising predictor and with correlation coefficients of about $r = 0.7$ are still of great value to breeders.

Economic and agronomic considerations

Mid-parent value. The mid-parent value is the predictor that is generally used in potato breeding programmes since the method is quick, cheap and easy. No time is lost with the production of hybrid seed and seedlings, and the data are available from experiments already performed with the clones of interest. If additional information is needed, the costs of trials is not likely to interfere with a large number of entries to be tested. Fur tuber yield at ware potato harvest, however, the relationship between the predicted progeny performance and the actual one was not good. This relation might be improved by carrying out harvests at intervals during the growth season, as reported earlier (Neele 1990). Although this procedure would increase the costs of land and above all labour, it provides an accurate estimate of the progeny yielding ability.

Table 6. Correlation coefficients of the progeny means of ware potato tuber yield for 4 years and the estimated progeny performance based on different prediction methods in various years. Correlations based on actual performance and prediction in the same year are printed in *italics*. ($df = 18$)

Prediction method		Tuber yield in			
		1986	1987	1988	1989
Mid-parent	1986	*0.16*	−0.12	0.24	0.43
	1987	0.03	*0.24*	−0.11	0.27
Test crosses	1987	0.78	*0.79*	0.69	0.67
	1988	0.71	0.68	*0.78*	0.75
Diploids	1988	0.04	−0.24	*−0.47*	−0.40
	1989	0.27	0.10	−0.21	*−0.34*
Selfs	1987	0.33	*0.25*	0.45	0.48
	1988	0.49	0.55	*0.30*	0.24
	1989	0.61	0.61	0.11	*0.12*

$P\ (r \geq 0.44) < 0.05$; $P\ (r \geq 0.56) < 0.01$

Diploids. The efforts and costs required to obtain a sufficiently large diploid progeny is already a problem. The occurrence of poor growing plants in diploid progenies makes it a poor predictor and disqualifies this approach. Many of the small plants hardly produced tubers, which were needed as seeds for the next years generation. The small plants were also affected by strongly growing neighbouring plants, which made it difficult to measure the genetic potential of these clones as well as that of their neighbours.

Selfed progenies. The production and maintenance of the selfed progenies did not raise major difficulties for the varieties and breedig lines used in this study. These clones, however, were selected for good male fertility. A large proportion of the population of potential parents barely produce pollen or are even male sterile. Therefore, a major drawback in using selfed progenies in comparison to the other predictors is that the possibilities of selfing are restricted to male-fertile clones. In addition, selfed progenies, apart from demanding the effort, provide no more information than the mid-parent value.

4x-2x Test-crosses. Test-crosses were found to offer good possibilities for evaluating the value as a breeding parent of potato clones. However, time is needed to carry out the test-crosses and to grow the seedlings. Moreover, many clones have to be tested per test-cross, even though we used a smaple size of only 30 clones per test-cross. Since four male testers were used for the evaluation of

Table 7. Ranges of correlation coefficients of the progeny means of the incomplete diallel with the sum of the GCA values of the mother and the father as estimated by test crosses with each of the testers separately or in six combinations of two diploid testers for characters determined during the growth season and during and after the harvests of 1987 ($df = 18$)

	Seed potato harvest		Ware potato harvest	
	One tester	Two testers	One tester	Two testers
Early season growth	−0.68–0.75	−0.52–0.78	−0.15–0.89	0.11–0.89
Number of stems	−0.55–0.41	−0.50–0.44		
Stolon length	0.92–0.95	0.93–0.95		
Plant appearance	0.55–0.94	0.81–0.96	0.72–0.83	0.75–0.82
Skin colour	0.89–0.91	0.89–0.91	0.85–0.90	0.89–0.90
Tuber shape	0.47–0.91	0.84–0.93	0.45–0.81	0.66–0.82
Regularity tuber shape	0.67–0.87	0.75–0.87	0.78–0.85	0.81–0.85
Eye depth	0.82–0.90	0.85–0.93	0.74–0.93	0.83–0.91
Tuber yield	0.85–0.97	0.89–0.96	0.40–0.82	0.68–0.84
Number of tubers	−0.23–0.78	−0.13–0.50	0.04–0.68	0.38–0.71
Prop. weight by tubers <30 mm	0.75–0.87	0.80–0.87	0.33–0.63	0.42–0.59
Number of tubers per stem	−0.35–0.78	−0.16–0.85		
Average tuber weight	0.83–0.89	0.85–0.91	0.61–0.81	0.69–0.81
Underwater weight			0.66–0.93	0.88–0.96

$P\ (r \geq 0.44) < 0.05$; $P\ (r \geq 0.56) < 0.01$

one parent clone, 120 clones had to be examined. This high number of clones would be a major restriction to the number of advanced breeding clones and varieties that can be studied. However, this number might be able to be reduced, since we observed that the correlation coefficients hardly decreased by using two (Table 7) instead of four tester clones (Table 5). In Table 7 1987 is taken as an example year the other years showed similar results. Only in the cases of poor or moderate prediction might the correlation coefficients found using two testers be lower. In addition, none of the six combinations of two testers were superior to the others. This means that only 60 clones per parent have to be tested, and this number will allow evaluation of a considerable number of entries. Furthermore, three of the testers were desynaptic (SY7, M6 and BE-62), the fourth, P680, synaptic, and since no differences were observed between prediction with synaptic or desynaptic testers, desynapsis might not be required.

Using only one tester clone, however, is not recommended since in that case lower correlation coefficients for the predictors were found for most characters, indicating the risk of incorrect parental choices (Table 7). Identification of a superior male tester was also not possible in these cases.

Conclusions

The parents used in this study presented a large variation in agronomical performance, maturity and genetic background. Therefore, the results obtained in this study are likely to be representative for breeding programmes in general.

For most of the characters studied, the general combining ability, GCA, was the major source of genetic variation between the hybrid populations. Although for the ware potato harvest the specific combining ability, SCA, was relatively more important, in almost all characters the GCA was the important one. For most characters, differences in the within-progeny variance could not be assigned to certain parents, but were the results of specific parental combinations. For characters with a predominant GCA for the within-progeny variance, it seems that this could be contributed to the time of tuberization and the distribution of the assimilates afterwards.

The seedling performance for tuber yield, average tuber weight and number of tubers did not show appropriate relation to field performance during the following the years. These results suggest that seedling performance should not be taken into consideration for progeny selection for the characters mentioned.

The mid-parent value, generally used in practice, provided proper predictions for almost all of the characters. A major exception was tuber yield at ware potato harvest. This means that if the seed potato harvest performance is the most important one, the performance of the progeny is satisfactorily predicted by the mid-parent value. At ware potato harvest, this estimate is likely to be of less value, particularly for tuber yield where the estimate did not show any significant relation to the actual value. A better predictor based on the traits of the parents themselves was found by using crop physiological components of the parental tuber yield (Neele 1990).

Progeny means of diploid and selfed offspring did not produce better estimates of the progeny performance than the mid-parent value. In addition, the diploid progeny was difficult to produce and to maintain over subsequent clonal generations. Therefore, the results suggest strongly that both methods should be not recommended.

The predictive ability of test-crosses with diploid 2n-FDR-pollen producing males seems to be at least as good as that of the mid-parent value, and for yield and underwater weight at ware harvest the test-crosses in this study were superior. A drawback of this method is the investment in the production of true seeds and seedlings, although this can be done together with crossing and seedling raising already routinely carried out in any potato breeding programme. Moreover, commercially interesting clones might arise as a spin-off of this prediction method.

Acknowledgements. The authors thank Prof. S. J. Peloquin for the opportunity to use the clones M6 and SY7, E. Jongedijk for the use of the clones BE-62, CE-10 and FB-107 and M. Wagenvoort for the clone P680. We are grateful to A.P. Vroegop for his contribution to the practical part in the experiments.

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