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Cross prediction in a potato breeding programme by evaluation of parental material

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Summary. It is shown that it is possible to obtain an indication of the parental value of heterozygous cultivars of potatoes for the characters breeders' preference, total tuber weight, mean tuber weight and number of tubers. Three methods of predicting the characteristics of progeny produced from particular parental cultivars were examined, namely: univariate cross prediction (based on mean and variance), mid-parent values and mid-self values. All provided some indication of which crosses would give superior progeny, but univariate cross prediction gave rankings which correlated most highly with observed performance in the second clonal year for the characters breeders' preference and total tuber weight. Interestingly, mid-self values gave the best predictions in the case of mean tuber weight and number of tubers. It is suggested that such predictions of 'parental value', especially when based on univariate cross prediction at the seedling stage, are worth carrying out in practical breeding programmes.

Key words: *Solanum tuberosum* – Parental value – Univariate cross prediction – Mid-parent – Mid-self value

Introduction

Following the earlier work on methods of cross prediction in *Nicotiana rustica* (Jinks and Pooni 1976, 1980; Pooni and Jinks 1985), the technique has been applied to a number of inbreeding crop species (Caligari et al. 1985; Snape and Parker 1986; Thomas et al. 1986). Such methods have also been shown to be appropriate for a clonally reproduced crop, namely the European cultivated potato, *Solanum tuberosum* (Caligari and Brown 1986; Brown and Caligari 1988). The use of cross prediction applied to a practical potato breeding situation was also shown to be a realistic alternative to the ineffective selection of individual clones in the early generations of potato breeding (Brown et al. 1988).

Cross prediction, as described above, involves hybridization of chosen parents and examination of a subset of the progeny from each cross, in order to estimate the parameters which form the basis of the prediction. This provides an extremely powerful approach compared with conventional methods, but would be even more effective if the predictions could be based directly on parental performance. Traditional biometrico-genetical techniques theoretically hold the promise of supplying this information. However, the tetraploid status of *S. tuberosum* combined with the fact that potential parents are almost invariably highly heterozygous complicates the basic assumptions of many of the biometrical techniques and, hence, makes such approaches less powerful in practical breeding than with diploid inbreeding species.

Other analytical methods are available, for example, the use of combining abilities (Griffin 1956; Sprague and Tatum 1942). Where general combining ability effects predominate, it is possible to predict reasonably accurately the properties of hybrid crosses according to the parents concerned. If, however, most variation is accounted for by specific combining ability, no predictions can be made without evaluation of individual cross combinations. Although such approaches, based on statistical rather than genetical considerations, have their uses

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and advantages, in many practical situations they do not offer satisfactory alternatives to the more genetically based ones.

Most combining ability studies on potatoes have been carried out using a number of test crosses. Half-diallel crossing designs were used by Killick (1976), while North Carolina II designs were employed by Plaisted et al. (1962) and Killick and Malcolmson (1973). All possible cross combinations were not completed by any of these authors due to problems of fertility and, therefore, missing cells had to be estimated. Problems of lack of fertility are well known in potatoes and thus led Tai (1976) to suggest the use of partial diallels (Kempthorne and Curnow 1961) in order to avoid the need to obtain every possible cross combination.

Using the diallel approach, a number of workers have investigated several characters of economic importance in potatoes. Many of these studies have concerned yielding ability where specific combining ability has been found to be relatively large (Plaisted et al. 1962; Killick 1976; Tai 1976). High specific combining ability for yield was found to be the result of high specific combining ability for number of tubers rather than mean tuber weight, which showed high general combining abilitiy (Tai 1976). From other characters examined, foliage maturity has shown high general combining ability (Killick 1976) as did resistance to the white potato cyst-nematode (Phillips and Dale 1982), starch content (Pika and Tarasenko 1985), *Streptomyces scabies* resistance (Pfeffer and Effmert 1985) and crisp fry colour (Chitsay 1984). Characters which have shown a predominance of specific combining ability include resistance to *Phytophthora infestans* (Killick and Malcolmson 1973), specific gravity of tubers (Plaisted and Patterson 1963) and tuber blackening after cooking (Dalianis et al. 1966; Pika et al. 1984).

In this paper the feasibility of using parental assessment to predict the performance of potato crosses is examined. Various types of predictions are compared with observations based on a subsample of seedlings from each cross and also by the performance of clones from the crosses in the advanced stages of a potato breeding scheme.

Materials and methods

Crosses were carried out and seed obtained in the spring and summer of 1981. Five parents, commercially grown cultivars – namely, (1) Pentland Ivory, (2) Baillie, (3) Wilja, (4) Cara and (5) Desiree – were used in a half-diallel crossing scheme. Progeny from the crosses were identified by the letter B followed by two integer numbers which indicated the two parents used (given above). Wilja was found to have very poor berry retention and it was therefore not possible to obtain seed from the self of this cultivar. All other crosses and selfs yielded sufficient quantities of seed.

One hundred seeds from each of the 14 crosses were sown in seed pans and transplanted to 10-cm square pots after 3 weeks of growth. Seedlings were then grown to maturity in an aphid-proof glasshouse. At harvest, tubers were assessed for breeders' preference, a visual assessment on a 1–9 scale with increasing preference associated with increasing score (Brown et al. 1984, 1987). The total tuber weight and number of tubers produced by each seedling were recorded, from which mean tuber weight was calculated. The largest tuber produced from each of 50 seedlings was retained for planting in the first clonal year.

In the first clonal year, plants were grown at Blythbank Farm, Peeblesshire (BB), in a completely randomized block with each cross being represented by 50 genotypes, each grown as a single plant. No data were collected from the first clonal year trial, which was grown purely to provide field-grown seed tubers for the second clonal year trial. In the second clonal year, 25 clones from each cross (350 genotypes) were taken at random for planting. However, there was a restriction imposed in that each of the clones used had to have produced at least six tubers. This restriction did not have a serious effect on the choice of clones because more than 95% of all plants complied with this criterion.

The 350 clones were planted in a single randomised block at BB and also at the Murrays farm in East Lothian (MURR). BB is the farm used by the Scottish Crop Research Institute (SCRI) for the multiplication of healthy potato seed tubers, while MURR is used by the Institute for yield trials. Each plot at each site consisted of three plants, planted 45 cm apart with a 120-cm gap between plots. Five plots of the parental clones were included in the randomization at each site.

The MURR trial was planted 2 weeks earlier than the BB trial. Before harvest, the BB plots were defoliated by a double application of sulphuric acid while the MURR plots were mechanically defoliated 21 days later. Hence BB had a short growing season than MURR. Both trials were mechanically harvested and the tubers from each plot hand-picked into boxes. While the tubers were still in the field, they were assessed for breeders' preference on a 1–9 scale. The produce was taken into store where the total tuber weight and number of tubers per plot were recorded.

In the third clonal year, a random sample 155 clones was identified and grown at MURR. No restrictions were imposed on the random sample and it did not contain any predefined number from each of the 14 crosses. Each clone was represented as a five-plant single drill plot in each of two completely randomised blocks. The trial was treated in the same way as the normal SCRI potato breeders' third clonal year trials and clones were discarded from this trial unless they complied to the usual selection criteria. The clones selected from this trial were incorporated into routine breeders' trials along with clones from the Institute's main potato breeding programme.

Results

The parents used in the half-diallel were included in the randomisation of the second clonal year trial. Each parent was grown at both BB and MURR and replicated four times at each location. From the analyses of variance (Table 1), breeders' preference scores were significantly greater ($P < 0.001$) at MURR than at BB. Similarly, total tuber weight, mean tuber weight and number of tubers were significantly greater ($P < 0.001$) at the MURR site. The parents used in this study were deliberately chosen to represent a range of early and late maturing cultivars which also produced a range of tuber numbers and sizes. The sites were also taken to represent 'seed' and 'ware' conditions, hence a completely fixed model was employed in the analysis. The effect of parents was significant for all variates when tested against the replicate error.

Inspection of the parental means at both sites (Table 2) and also their ranking within each site indicated the sources of the detected interactions. At BB, Wilja was the highest yielding parent (total tuber weight) and Cara was the lowest yielding. When grown at MURR, however, Cara was the highest yielding whereas Wilja only ranked fourth. Inspection of the rankings within sites for mean tuber weights suggest that Wilja was largely responsible for the interaction, but Desiree also showed such effects. Wilja is a cultivar which is early bulking while Cara tends to mature later than the other parents (Anon 1987). The interactions for yield and yield components are therefore partially accounted for by this wide range in maturity and bulking rates, coupled with the contrasting long and short growing season of MURR and BB, respectively.

Mean squares from the analyses of variance of the ten progenies (i.e. the 5×5 half-diallel ignoring the selfs) grown at BB and MURR are shown in Table 3. The effect of progenies was partitioned, according to the method of Griffin (1956), into general (GCA) and specific (SCA) combining ability. The interaction of sites with SCA was consistently smaller than the error (the within-progeny variation), and hence the latter term was used to test the other interaction and also the main effects. GCA effects were significant ($P<0.001$) for all four variates while SCA was only significant ($P<0.001$) for mean tuber weight. The interaction of sites with GCA was significant for total tuber weight ($P<0.05$) and highly significant for mean tuber weight ($P<0.001$).

The preponderance of GCA effects indicated the possibility of predicting the performance of crosses according to the phenotype of the parents. Three methods of estimating progeny performance were therefore considered: (a) univariate prediction based on the mean and variance of performance of seedlings (as detailed by Caligari and Brown 1986); (b) prediction based on mid-parent values (which effectively assumes a simple additive genetic model is sufficient); and (c) prediction based on mid-self values. The ranking of the ten crosses, according to performance averaged between BB and MURR in the second clonal year is given, along with the ranks according to three prediction methods, in Table 4. Clearly all prediction methods provide some indication as to which are the superior crosses. The accuracy of prediction was investigated further by correlating the three prediction methods with the observed progeny performance in the second clonal year (Table 5). All correlation coefficients were positive, although more than half of them formally fell short of statistical significance. Univariate prediction based on the mean and variance of crosses as seedlings provided the best indication of breeders' preference, while the mid-self value was least accurate for this character. Total tuber weight was also

Table 1. Mean squares from the analyses of variance of the character, breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) per plant recorded at two sites, Blythbank (BB) and Murrays (MURR), for five parent cultivars

Source	df	Pref	TTW	MTW	NT
Sites	1	6.40***	2.380***	3,019***	3.80***
Parents	4	9.49***	0.076	63**	10.21***
Sites × Parents	4	1.84	0.417***	69***	24.90***
Error	31	1.192	0.0404	10.8	0.758

** = $0.01 > P > 0.001$
*** = $P < 0.001$

Table 2. Average value (plus ranks, in parentheses), of five parent clones used in a half-diallel crossing scheme, for the characters breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) when grown at two sites, Blythbank (BB) and Murrays (MURR)

	Pref	TTW (kg)	MTW (g)	NT
BB				
1 Pentland Ivory	4.25 (3)	1.22 (4)	119 (2)	10.3 (4)
2 Baillie	4.50 (2)	1.61 (2)	114 (3)	15.4 (1)
3 Wilja	6.00 (1)	1.67 (1)	128 (1)	13.0 (2)
4 Cara	3.75 (4)	0.90 (5)	106 (4)	8.5 (5)
5 Desiree	2.75 (5)	1.29 (3)	105 (5)	12.3 (3)
MURR				
1 Pentland Ivory	5.75 (2)	1.73 (2)	176 (1)	9.8 (5)
2 Baillie	4.25 (4)	1.73 (2)	162 (3)	10.7 (4)
3 Wilja	6.75 (1)	1.69 (4)	152 (5)	11.1 (3)
4 Cara	3.75 (5)	2.07 (1)	153 (4)	13.5 (1)
5 Desiree	4.75 (3)	1.09 (5)	168 (2)	11.3 (2)

Table 3. Mean squares from the analysis of variance for total tuber weight (TTW), mean tuber weight (MTW), number of tubers (NT) and breeders' preference (Pref.) recorded on the progenies of a 5×5 half diallel ignoring selfs. (G.C.A. = general combining ability; S.C.A. = specific combining ability). The error item includes "clones within progenies" plus "clones within progenies × sites"

Source	d.f.	TTW	MTW	NT	Pref.
G.C.A.	4	32.97***	9.86***	4,581***	11.53***
S.C.A.	5	3.41	8.24***	444	4.92
Sites × G.C.A.	4	4.70*	15.78***	318	2.15
Sites × S.C.A.	5	0.12	1.18	174	1.37
Error	480	1.93	1.73	227	1.92

* = $0.05 > P > 0.01$
*** = $P < 0.001$

Table 4. Progeny rankings based on (a) prediction made on seedlings in the glasshouse (based on progeny mean and phenotypic variance); (b) mid-parent values; (c) mid-self values; and (d) observed performance of progenies in the second clonal year. The characters recorded were breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT)

Cross	Pref.				TTW				MTW				NT			
	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)
B12[a]	7	5	4	9	10	6	8	10	8	3	3	2	10	7	8	9
B13	8	1	7	1	8	6	8	7	2	3	4	8	6	8	10	7
B14	10	6	10	10	9	10	10	8	1	5	2	1	2	10	9	10
B15	9	6	9	7	7	9	7	9	6	1	1	3	9	9	7	8
B23	5	2	1	2	3	1	3	3	4	6	10	5	1	1	5	4
B24	4	8	3	8	4	4	6	5	2	10	8	9	5	3	4	1
B25	6	8	2	6	6	3	1	6	7	7	7	7	3	2	1	6
B34	3	3	6	4	5	4	5	4	5	7	9	10	4	5	6	5
B35	1	3	4	4	1	2	1	1	10	4	6	4	7	4	3	3
B45	2	10	8	2	2	8	4	1	9	9	5	5	7	6	2	2

[a] The numbers in the codes for the crosses stand for the parents involved which were: 1. Pentland Ivory, 2. Baillie, 3.Wilja, 4. Cara and 5. Desiree

Table 5. Phenotypic and rank coefficients obtained by correlation of predicted (based on mean and variance of seedlings (Seed), mid-parental values and mid-self values onto observed values (mean of progeny at Blythbank and Murrays) for the characters breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT)

	Pref.	TTW	MTW	NT
Phenotypic correlation				
Seed	0.48	0.90**	0.46	0.11
Mid-parent	0.41	0.55	0.40	0.71*
Mid-self	0.26	0.76*	0.68*	0.79*
Rank correlations				
Seed	0.48	0.95***	0.19	0.11
Mid-parent	0.39	0.51	0.48	0.71
Mid-self	0.16	0.72	0.68	0.80

* = $0.05 > P > 0.01$
** = $0.01 > P > 0.001$
*** = $P < 0.001$

most accurately estimated by seedling evaluation, but here mid-self value provided a better estimation of progeny worth than the mid-parent value. The most accurate estimation for both yield components was found from the mid-self values (accounting for 46% and 62% of the total variation in the second clonal year for mean tuber weight and number of tubers, respectively).

The above predictions were based on the performance of parents, selfs and also progenies averaged over the two sites. However, the five parental clones were of contrasting types and resulted in large genotype by environment interactions. Correlation between predicted (based on mid-self and mid-parent) and observed at each site separately showed a consistent tendency for higher coefficients between predicted and observed at a common location rather than predicted in one environment and observed in the other (Table 6). Some of these relationships were large. When the predictions, based on mid-parent values, were made from parental data collected at BB, correlation between predicted and observed were higher at BB than MURR for breeders' preference, total tuber weight and mean tuber weight, and equal for number of tubers. When predictions were based on parental performance at MURR, however, correlation coefficients between predicted and observed were always of higher magnitude, in a number of cases significantly so, at MURR rather than at BB. An almost identical result was found when the mid-self predictions were examined. Overall therefore, prediction by mid-parent of mid-self is affected, not unexpectedly, by the environment in which either the parents or self are evaluated or progenies are grown.

When GCA is large in relation to SCA, it is not only possible to identify the superior crosses but also the better parents. Inspection of the parental cultivar performance, the performance of third clonal year progenies in which that parent featured, self values and also the average performance of seedlings in which the parent features (Table 7) showed that again a degree of prediction was possible. Wilja was assessed as the better parent according to breeders' preference at the seedling stage, the better parent on parental evaluation and also the parent which showed highest mean progeny performance in the second clonal year. Pentland Ivory was the lowest yielding parent, was the parent with the lowest yielding self, produced seedlings with lowest yield and also gave the lowest GCA. Wilja was found to be highest yielding and was ranked second, first, and second for total tuber weight when seedlings, parents and selfs, respectively

Table 6. Phenotypic correlations at the two sites, Blythbank (BB) and Murrays (MURR) between predicted (based on mid-parent and mid-self) and observed values of ten crosses for breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT). Coefficients in italics are those where predicted and observed were in a common environment

	Pref.		TTW		MTW		NT	
	BB	MURR	BB	MURR	BB	MURR	BB	MURR
Based on mid-parent values								
BB	*0.31*	0.25	*0.27*	0.01	*0.47*	−0.17	*0.31*	0.31
MURR	0.35	*0.40*	0.02	*0.35*	−0.12	*0.57*	0.50	*0.53*
Based on mid-self values								
BB	*0.37*	−0.21	*0,63**	0.78**	*0.26*	−0.54	*0.48*	0.54
MURR	0.04	*0.59*	0.82**	*0.84***	−0.11	*0.82***	0.67*	*0.74***

* = $0.05 > P > 0.01$
** = $0.01 > P > 0.001$

Table 7. Parental worth determined by the average of all offspring grown as seedlings (Seed), parental expression (Parent) and average expression of selfs along with progeny performance in the second clonal year (SCY). The five parental lines were Pentland Ivory (PI), Baillie (Ba), Wilja (Wi), Cara (Ca) and Desiree (De) and the characters recorded were breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT)

	Seed	Parent	Self	SCY
Pref.				
PI	0.079 (5)	5.00 (2)	2.55 (5)	3.91 (5)
Ba	0.181 (4)	4.37 (4)	3.48 (1)	4.06 (3)
Wi	0.245 (1)	6.37 (1)	3.22 (2)	4.46 (1)
Ca	0.198 (3)	3.75 (5)	2.68 (4)	4.05 (4)
De	0.240 (2)	4.50 (3)	2.84 (3)	4.19 (2)
TTW				
PI	0.029 (5)	1.47 (5)	0.67 (5)	1.24 (5)
Ba	0.168 (4)	1.67 (2)	0.96 (3)	1.38 (4)
Wi	0.226 (2)	1.68 (1)	0.98 (2)	1.55 (1)
Ca	0.213 (3)	1.49 (4)	0.88 (4)	1.43 (3)
De	0.262 (1)	1.59 (3)	1.06 (1)	1.45 (2)
MTW				
PI	0.216 (2)	150 (1)	49 (5)	123 (1)
Ba	0.161 (4)	144 (4)	101 (3)	110 (4)
Wi	0.169 (3)	142 (2)	97 (4)	107 (5)
Ca	0.237 (1)	129 (5)	112 (2)	115 (2)
De	0.068 (5)	139 (3)	129 (1)	112 (3)
NT				
PI	0.082 (4)	10.1 (5)	6.2 (5)	11.2 (5)
Ba	0.208 (1)	13.1 (1)	11.2 (2)	13.8 (4)
Wi	0.175 (2)	12.0 (2)	10.4 (4)	14.9 (1)
Ca	0.140 (3)	11.0 (4)	10.8 (3)	14.0 (3)
De	0.078 (5)	11.8 (3)	11.9 (1)	14.2 (2)

were examined. The yield components were also dominated by the parent Pentland Ivory which consistently produced large but few tubers (highest mean tuber weight at MURR and second highest at BB) relative to the other parents.

Discussion and conclusions

Analyses of the 5 × 5 half-diallel resulted in a predominance of GCA effects for breeders' preference, total tuber weight and number of tubers while SCA effects were large for mean tuber weight. This was in contrast to results found by some other workers (Plaisted et al. 1962; Killick 1976; Tai 1976), although Rowell et al. (1986) found significant GCA for yield and tuber characters when hybrids between 'Neotuberosum' and *S. tuberosum* were examined. This was the case when Masson (1985) examined interploidy crosses. In both these studies, the parental material was genetically diverse, and in cases where a broad genetic base exists between parents, SCA effects are expected to be reduced (an example in potatoes is given by Phillips and Dale 1982). Although all parents used in this study were *S. tuberosum* spp. *tuberosum,* they were from different origins. The clones Pentland Ivory and Baillie were from the SCRI breeding programme, Desiree and Wilja were from Dutch breeding programmes and Cara was bred at the Oak Park Research Institute, Eire. They therefore represent a moderately wide genetic base.

It was possible to obtain an indication of progeny worth by using univariate predictions based on seedling performance, evaluation of parental clones and hence obtaining mid-parent values, and by studying mid-self values. Univariate cross prediction based on the seedling stage gave closest agreement with observed performance in the second clonal year for two of the characters. These were breeders' preference and total tuber weight, which many breeders would agree are of most practical importance. When the predictions for mean tuber weight and number of tubers were examined, it appeared that mid-self values gave the best indication of progeny performance. The predictions were, however, greatly influenced by the environment in which they were made relative to the environment that they would ultimately be destined for. Predictions when parents were grown at MURR were most useful in predicting performance of progeny at that site and a similar situation was found for BB. In other words, if parental predictions are to be useful in a potato breeding programme then, as in other situations, it is essential that the parents are evaluated under the environmental conditions that the eventual cultivars will be grown.

Results did, however, show that parental predictions even made at limited sites would be useful, if only to eliminate the worst parents. Clones from the half-diallel study were entered and evaluated alongside clones from the normal breeding material from the SCRI potato breeding programme. These clones have been evaluated in the system for 3 years and clones have only continued in the scheme if they satisfy the standard selection criteria. From amongst the five clones examined, Pentland Ivory was shown to be the 'worst' parent for all characters except mean tuber weight. After three rounds of selection, only three clones survived in which Pentland Ivory featured as a parent. Predictions based on seedling performance and also mid-parent performance ranked the cultivar Baillie fourth and this parent contributed only four clones to the standard SCRI fifth-clonal year trials. From the predictions, the remaining three parents were considered to have greater merit. This was again reflected in practice in that Wilja contributed eight clones, Desiree contributed nine clones and Cara contribution ten clones to this stage in the breeding scheme. The ranking of parental worth according to either seedling performance, mid-parent on mid-self performance did not give an exact relationship to the number of survivors at the later stages in a breeding scheme but did give a reasonable guide to the eventual contribution. This becomes even more evident when it is noted that selection also actually involved cooking quality characters which had not been taken into account in the predictions. It is interesting to note, however, that cross prediction of seedlings can provide a good prediction of the better parents as well as identifying the superior cross combinations. In addition, mid-parent or mid-self values allow at least the worst parents to be identified.

Mid-self values provided a good prediction of progeny worth and, in most cases, a more accurate estimation than the mid-parent. Estimating parental worth using a single test cross was found to correlate highly with the estimation where four test crosses were used (Rowell et al. 1986). It is possible, therefore, that selfing has much the same effect as a single test cross system. Although mid-self values provided better predictions than mid-parent, it should be remembered that evaluation of selfs will be more time- and labour-intensive than simply evaluating parents. Neither mid-parent or mid-self predictions were as good in predicting either total tuber weight or breeders' preference as evaluating seedlings in the glasshouse. Since these two characters can be considered to be of paramount importance, particularly breeders' preference which incorporates many of the features that make up a successful potato cultivar, then it would suggest that this could provide a useful basis for selecting between potential future parental material. It is particularly appealing since it can be combined with more usual cross prediction aims of simply assessing the potential of the progeny themselves.

Overall, therefore, it is suggested that this method of parental assessment provides a useful first screen in a breeding programme in order to avoid using undesirable parents. This would allow valuable time and resources to be concentrated on crosses with a higher probability of producing desirable genotypes.

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