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Plant breeding

Agronomic and technological evaluation and selection of tetraploid clones of potato (*Solanum tuberosum* L) originating from diploid populations

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Summary — Sexual polyploidization with 2*n* gametes was used to return to the tetraploid level at the end of a breeding programme at the diploid level. Agronomic evaluation (yield and technological traits) of 518 tetraploid clones originating from diploids (TDO) was performed over a 3 year period. A 'modified augmented design' (MAD) was used. The clones were tested without replications; control varieties in Latin squares allowed us to compute adjusted values. Adjustments were low except in 1992. Using their adjusted values, clones were selected with an index combining yield and dry matter content with values of Bintje and Claustar as a threshold. The average rates of selection after the first, second and third screenings were 40, 52 and 44%, respectively. Few clones had a higher yield than the controls but their dry matter content was high. Variability for other traits was high.

***Solanum tuberosum* L = potato / diploid / 2*n* gametes / modified augmented design**

Résumé — Évaluation agronomique et sélection de clones tétraploïdes de pomme de terre (*Solanum tuberosum* L) issus de diploïdes. *La dernière étape d'un schéma de sélection de la pomme de terre au niveau diploïde est le retour au niveau tétraploïde souvent réalisé par polyploïdisation sexuelle grâce aux diplogamètes (gamètes* 2n*). L'évaluation agronomique (rendement et caractères technologiques) de 518 clones tétraploïdes ayant au moins un parent diploïde (TOD) a été entreprise sur 3 années d'expérimentation au champ. Un dispositif expérimental appelé* "Modified augmented design" *a été utilisé : les clones sont testés sans répétition et la présence de témoins disposés en carrés latins permet de calculer des valeurs ajustées. Les ajustements nécessaires n'étaient pas très élevés en comparaison avec les valeurs mesurées, sauf en 1992. À partir de leur valeur ajustée, les clones ont été sélectionnés par rapport à un index tenant compte du rendement commercial et de la teneur en matière sèche avec comme seuil les valeurs de Bintje et de Claustar. Les taux moyens de sélection après la première, deuxième et troisième évaluation ont été de 40, 52 et 44% respectivement. Peu de clones présentaient un rendement supérieur aux témoins mais leur teneur en matière sèche était élevée. La variabilité pour les autres caractères était importante.*

Solanum tuberosum *L = pomme de terre / diploïde / gamètes* 2n */ dispositif MAD*

* Correspondence and reprints

INTRODUCTION

A scheme for breeding tetraploid potato (*Solanum tuberosum* subsp *tuberosum*) at the diploid level was proposed by Chase (1963). This offered the possibility of introducing traits from other diploid species and of simplifying genetic segregations to some extent. The last step of the scheme consists on returning to the tetraploid level. A widely used method is sexual polyploidization by means of gametes with sporophytic chromosome number (2*n* gametes) which result from meiotic nuclear restitution mechanisms (Mendiburu and Peloquin, 1977). This can use unilateral (4*x* x 2*x* or 2*x* x 4*x*) or bilateral (2*x* x 2*x*) polyploidization. Numerous studies dealing with the use and genetics of tetraploids originating from diploids have been published and one of the most recent reviews was written by Tai (1994). The main fact is that tetraploid progenies originating from diploids (TDO) are very vigorous, and outyield the parents and standard varieties. However other traits such as tuber characteristics are not as good. As far as we know, only 2 or 3 commercial varieties have been produced directly from sexual polyploidization.

The experiment reported in this paper was aimed at screening clones obtained from TDO progenies. The various parental genotypes were not selected for special purposes such as resistance. The only possible use of the material was thus for adaptation criteria (north west European or Mediterranean area). However, it was necessary to evaluate their agronomic value as soon as possible, which prevented us from making replications due to the small number of tubers for each clone and the high number of clones. A special design was thus applied.

MATERIALS AND METHODS

Materials

A total of 518 clones were screened. They belonged to 3 types: TD from crosses 4x x 2x; DT from 2x x 4x; and DD from 2x x 2x.

The 428 TD belonged to 102 progenies from 24 tetraploid females and 29 diploid males producing 2*n* pollen. The 48 DT originated from 22 progenies from 8 diploid females producing 2*n* eggs and 5 tetraploid males. Diploid parents had (*S tuberosum* dihaploid x diploid species) background, with *S phureja* species for 24 of them, *S stenotomum* for 6, *S chacoense* for 3 and *S spegazzinii* for 1. Eight diploid clones were selected for the production of 2*n* gametes only and were provided by IvP-Wageningen (NL) and the University of Wisconsin (USA). Other diploid clones selected from our own programmes were chosen not only for production of 2*n* gametes but also for their rather good adaptation to French agronomic conditions (Rousselle-Bourgeois and Rousselle, 1992). Tetraploid parents were either varieties or advanced clones.

The 42 DD clones belonged to 23 progenies. They appeared at random within progenies which were designed for breeding at diploid level.

The clones had previously been selected over a 3 year period for their earliness, tuberization and tuber aspect (shape, eyes, skin and size).

Control varieties in the experimental design were representative of the usual standards: early (*eg*, Fanette); mid-early and ability for processing (*eg*, Bintje); or mid-early and high yielding (*eg*, Claustar).

Experimental design

The experimental design was suggested by the modified augmented design proposed by Lin and Poushinsky (1983). Experimental fields were divided into 3 x 3 Latin squares ; in each of them 3 control varieties determined 9 whole plots in which 9 tested clones were distributed at random (fig 1). The individual plots (tested clone or control variety) were planted with 22 tubers (2 rows of 11). The distance between plants within ridges was 32 cm. There was a distance of 75 cm between ridges. Results concern 3 years of experimentation at Ploudaniel (western part of France) on sandy silt soils with a high level of organic matter: 1991 (5 Latin squares, LS1 to LS5); 1992 (3 Latin squares, LS1 to LS3); and 1993 (2 Latin squares, LS1 and LS2). Usual husbandry practices were applied, such as weeding and protection against late blight. Planting took place around 15 April and harvest was performed at the beginning of September. Clones from other programmes were included in some trials in order to fill up all the plots; their results will not be presented here.

In the equations for analysis, the different elements were: i = 1 to 3, row number; j = 1 to 3, column number; X_{ij} = value of the control variety in the ith row and the jth column of the Latin square; $\bar{X}_{ij}$ = mean of the control variety X_{ij} in the whole Latin square; p = 3, number of control varieties; and Y_{ijk} = value of the kth clone in the ijth whole plot.

For each measured trait (1a, 1b, 2a, 2b, 4, 7 in the list below), the first step of the statistical analysis was the analysis of the Latin squares on a control plot basis, giving mean squares for rows, columns and error. An adjustment and an adjusted value Y'_{ijk} were computed for each clone, as proposed by Lin *et al* (1983).

1) If the row or column mean square was superior to the error mean square, a 'design adjustment' was calculated:

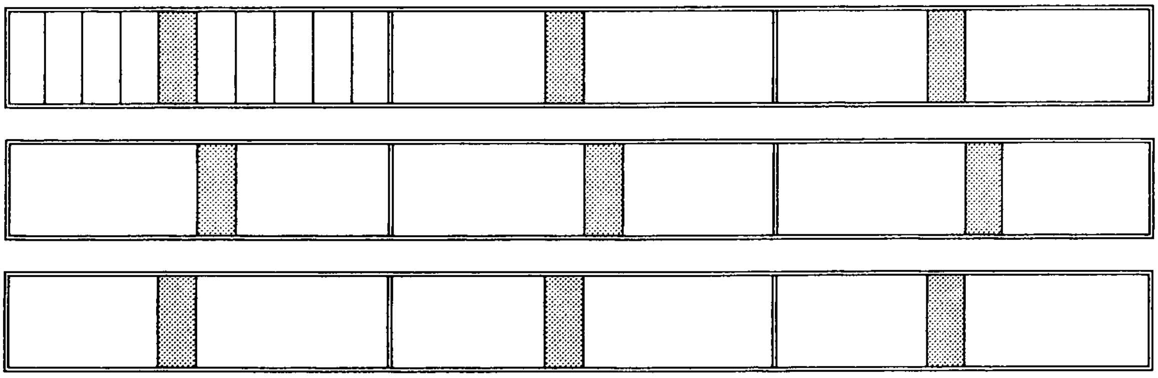

Fig 1. Design of one 3 x 3 Latin square. ▣ Whole plot ij (including 1 control variety and 9 tested clones); ▒ Control variety X_{ij} (subplot) distributed in Latin square; □ Tested clone T_{ijk} (subplot) distributed at random.

$$Y'_{ijk} = Y_{ijk} - (R_i + C_j)$$

where

$$R_i = \sum_j X_{ij} / p - \sum_i \sum_j X_{ij} / p^2$$

and

$$C_j = \sum_i X_{ij} / p - \sum_i \sum_j X_{ij} / p^2$$

2) If the error mean square was superior to the row and column mean square, a 'regression adjustment' was used:

$$Y'_{ijk} = Y_{ijk} - b(X_{ij} - \bar{X}_{ij})$$

where

$$b = \sum_i \sum_j (\bar{Y}_{ij.} - \bar{Y}_{...})(X_{ij} - \bar{X}_{ij}) / \sum_i \sum_j (X_{ij} - \bar{X}_{ij})^2$$

Adjusted values were used in further steps of selection.

Data

The characters observed were as follows.

1a) Total yield in kg; 1b) marketable yield (grade > 35 mm) in kg.

2a) Total number of tubers; 2b) number of tubers of marketable size.

3) Mean tuber weight in g as 1b/2b.

4) Dry matter content estimated using the Von Scheele *et al* (1936, in Burton, 1989) regression based on underwater weight of samples of approximately 5 kg.

5) Ability to produce chips (French fries). After storage at 9°C with sprout inhibitor application, 30 cylindrical chips were fried in February and graded into 3 classes (dark, medium and light). The parameter value was given using an index which was equal to (number of light chips + 0.5 [number of medium chips]). The index varied from 0 (inability) to 30 (full ability).

6) Cooking quality. After harvest, 4 tubers were cooked in water, and blackening and sloughing were scored on the same scale as for the French official registration of varieties: 0 (very blackened) to 3 (no blackening) scale and 0 (high sloughing) to 2 (no sloughing) scale.

7) Susceptibility to shock damage. This was assessed with a pendulum, following the method described by Rousselle and Gravoueille (1995) and measured by absorbed energy in mJ (10^{-3} J).

Observations were performed on plots during the growing period (foliage defects) and at harvest time (tuber characteristics and defects).

Selection plan

As illustrated in figure 2, thresholds based on an economic index were applied for the selection plan. Marketable yield or marketable mean tuber weight and dry matter content were considered. The thresholds used were values of the Bintje and Claustar varieties which are the usual standards for north west France and Mediterranean areas, respectively. We selected clones that were superior to (Bintje + Claustar)/2 for both characters (part D), clones with a higher dry matter content than Bintje, whatever their yield or tuber weight (part C), and clones with a higher yield or mean tuber weight than Claustar, whatever their dry matter content (part E).

RESULTS

Analysis of the experimental design

The analysis of the Latin squares on the values of the control varieties showed very few significant mean squares for variety effect, and only 5 cases of significant effects of column (total and

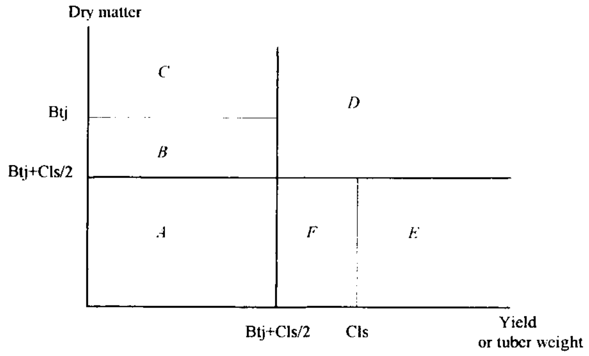

Fig 2. Selection plan for the TDO clones according to their values for marketable yield or mean tuber weight and dry matter content compared to those of Bintje (Btj) and Claustar (Cls). Clones were selected when in part C, D or E.

marketable yield in 1992-LS2 and 1992-LS3, dry matter in 1991-LS3), and none for row (table I). This could be due to the low number of degrees of freedom, which resulted in a high critical value of F (19.00). Out of the 52 cases of adjustment presented in table I, 17 were of regression type and 35 of design type.

All the adjustments were computed. However, some of them were small compared to the observed values. Table II gives the number of adjustments lower than 1 kg for yield, 10 for number of tubers and 0.50% for dry matter content. These values may be regarded as close to the error of measurement. In 1991 and 1993 about 2/3 of the corrections belonged to this group. This means that the experimental designs were rather homogeneous. In contrast, adjustments were high in 1992 because the columns were heterogeneous (field effect).

Clones with the best results in the first trial were selected and evaluated a second time in the following year, and in some cases, for one further year. Ranks were assigned for each year and each trait to the clones which were screened over 2 or 3 years, and Spearman's coefficients of correlation were computed. They were all highly significant (table III) except those for the yield of the small group first evaluated in 1992 and then in 1993. The ranking of the clones was rather consistent over the years.

Selection

Over the 3 years of experimentation, the clones were evaluated once (354), twice (89) or 3 times (75). The selection plan was applied for all the clones on trial in a given year. In 1992 the thresholds were increased by 10% because values of the controls were low and resulted in too many selected clones. In 1993, the choice was made more accurate for clones that had already been on trial once or twice by eliminating those with absorbed energy greater than 700 mJ, index for chips less than 30 and zero scores for blackening and sloughing, or other important defects, such as cracking, early sprouting or high susceptibility to late blight or common scab.

Figures concerning evaluated and selected clones are shown in table IV for each year, each group of genotypes and each level of evaluation. In all, 518 clones were evaluated. The average rates of selection within the first, second and third screening were respectively of 40, 52 and 44%. Percentages were variable between groups; only 13% of DT in 1991 and as much as 64% of TD, on the first evaluation in 1993, were kept. In 1993, 87% of the clones under third evaluation would have been kept following the usual threshold. Other clones were rejected for high absorbed energy (12), for frying and cooking (6), for other defects (12) or because they did not go through both selection plans (5) ; this led to a 41% rate of selection.

As illustrated by the 1991 results, most of the selected clones belonged to part C of the selection diagram (fig 3). Very few presented a yield higher than (Bintje + Claustar)/2 or Claustar; their main value was relatively high dry matter content. Choices depending on marketable yield or on mean tuber weight were consistent: 121 out of 148 clones were selected by both thresholds in 1991.

The variability for the different traits under evaluation, which was quite high, is presented in table V. Some TDO clones had a high productivity which was often due to the high number of tubers with a proportion of marketable tubers lower than in control varieties. Due to the use of an index combining several characters, we were able to preserve good variability for the different traits as illustrated by the values of the clones under second or third screening in 1993.

DISCUSSION AND CONCLUSION

The design adjustment was used in most cases, but the regression adjustment had to be applied sometimes. Lin *et al* (1983) discussed the relative efficiency of estimation of *b* either by regressing control subplots on the control plots or by regressing the means of all the test subplots

Table I. Values of the mean squares for control varieties (Var), rows (Ro), columns (Co) and error (Er) and type of adjustment (Adj) for 6 traits in the Latin squares of 1991, 1992 and 1993.

Year and Latin square	*Total yield (kg)*	*Marketable yield (kg)*	*Total No of tubers*	*No of marketable tubers*	*Dry matter content (%)*	*Absorbed energy (mJ)*
1991 LS 1						
Var	84.11	113.38	11 256	2 692	2.17*	
Ro	8.80	8.16	1 431	268	0.07	
Co	1.37	0.70	2 507	919	0.53	
Er	8.09	6.75	1 140	185	0.10	
Adj	Reg	Reg	Des	Des	Des	
1991 LS 2						
Var	4.75	20.02	76 169*	22 233*	24.42*	
Ro	4.54	3.05	5 682	1 089	0.04	
Co	3.34	3.27	381	569	0.55	
Er	6.88	7.25	2 410	620	0.06	
Adj	Reg	Reg	Des	Des	Des	
1991 LS 3						
Var	110.33	148.21	23 070*	1 290	8.25*	
Ro	4.67	4.98	495	241	0.14	
Co	5.92	5.77	1 125	1 364	4.40*	
Er	9.95	8.22	467	127	0.10	
Adj	Reg	Reg	Des	Des	Des	
1991 LS 4						
Var	24.25	24.47	0	744	6.57*	
Ro	7.45	7.71	27	262	0.54	
Co	3.39	2.86	57	25	0.26	
Er	20.48	19.79	903	675	0.04	
Adj	Reg	Reg	Reg	Reg	Des	
1991 LS 5						
Var	136.44	143.72	4 042	1 083	4.17*	
Ro	19.76	18.97	832	270	0.86	
Co	10.22	10.42	225	102	0.31	
Er	17.26	16.44	305	206	0.20	
Adj	Reg	Reg	Des	Des	Des	
1992 LS 1						
Var	4.24	1.59	19 732*	10 191*	17.88*	
Ro	2.56	3.30	80	31	0.88	
Co	33.87	35.20	137	739	0.36	
Er	8.36	8.43	193	155	0.16	
Adj	Des	Des	Reg	Des	Des	
1992 LS 2						
Var	0.14	0.89	16 240*	7 753	14.95*	
Ro	1.12	0.73	2 350	599	0.20	
Co	86.11*	81.35*	4 300	2 351	0.17	
Er	0.29	0.16	777	663	0.03	
Adj	Des	Des	Des	Des	Des	
1992 LS 3						
Var	7.71	2.94	26 120*	11 972*	13.18	
Ro	7.73	7.44	37	65	0.22	
Co	102.10*	103.00*	547	919	1.06	
Er	4.79	4.56	140	56	0.96	
Adj	Des	Des	Des	Des	Des	
1993 LS 1						
Var	11.05	17.03	18 576*	9 948*	7.99	5 096
Ro	55.25	56.27	1 942	993	0.42	1 194
Co	1.30	1.27	122	65	0.26	201
Er	4.28	4.28	581	356	0.62	294
Adj	Des	Des	Des	Des	Reg	Des
1993 LS 2						
Var	106.86*	113.32*	7 257	5 224	10.92*	6 878*
Ro	2.91	1.88	1 037	356	1.18	96
Co	0.05	0.02	92	12	0.35	562
Er	3.13	2.80	914	525	0.19	257
Adj	Reg	Reg	Des	Reg	Des	Des

Reg = regression adjustment; Des = design adjustment. * Significant effect ($\alpha = 5\%$, $F = 19.00$).

Table II. Values of minimum (min) and maximum (max) adjustments (adj) compared to minimum (min) and maximum (max) observed values and number of adjustments that could be considered as low for 6 traits in the Latin squares of 1991, 1992 and 1993.

	Total yield (kg)	*Marketable yield (kg)*	*Total No of tubers*	*No of marketable tubers*	*Dry matter content (%)*	*Absorbed energy(mJ)*
1991 (54 subplots)						
Min value	16.05	13.70	149	131	14.47	
Max value	49.40	48.65	745	446	23.55	
Min adj	–4.77	–4.83	–54	–37	–1.56	
Max adj	5.30	5.26	54	30	1.01	
Low adj	37	35	18	35	40	
1992 (36 subplots)						
Min value	6.75	3.80	102	92	12.36	
Max value	35.65	34.00	580	404	28.48	
Min adj	–7.56	–7.79	–56	–35	–0.94	
Max adj	8.01	7.98	72	47	0.81	
Low adj	5	4	13	11	25	
1993 (18 subplots)						
Min value	21.30	16.95	154	139	14.33	601
Max value	45.00	43.35	675	408	24.14	744
Min adj	–5.38	–5.26	–27	–23	–0.31	–8
Max adj	4.62	4.63	35	23	1.48	4
Low adj	18	11	6	12	13	15

Low adj = number of adjustments < ± 1.00 kg for yield, < ± 10 for No of tubers, < ± 0.5% for dry matter content, < ± 5 mJ for absorbed energy.

in the whole plots on the control plot. They concluded that the latter "is stable and safe under a wide range of genetic variations among the test lines". They noticed that the regression method of adjustment can be used in practice because test lines are randomized. From a strict statistical point of view, using only 1 control variety would be more accurate but from the biological point of

Table III. Spearman's coefficient of correlation between ranks of the clones compared for 2 different screening years.

	No of clones	*Total yield*	*Marketable yield*	*Total No of tubers*	*No of marketable tubers*	*Dry matter content*
1st screening 1991 2nd screening 1992	148	0.38*	0.53*	0.61*	0.52*	0.68*
2nd screening 1992 3rd screening 1993	76	0.36*	0.51*	0.54*	0.58*	0.63*
1st screening 1991 3rd screening 1993	73	0.50*	0.52*	0.68*	0.64*	0.66*
1st screening 1992 2nd screening 1993	16	0.09	–0.14	0.65*	0.56*	0.78*

* Significant $\alpha = 1\%$.

view, it is safer to get the response of several cultivars to avoid specific behaviour (Lin and Poushinsky, 1983).

The 'modified augmented design' (MAD) proved to be reliable in screening material for agronomic adaptation when replications were not possible. It is now widely used in our laboratory in other programmes in which the number of genotypes to be screened is high. Evaluations will be reduced to 2 years and the second one will be performed elsewhere, for instance, in northern France. We use mainly 4 x 4 or 5 x 5

Table IV. Results of selection of each year, each genetic group and each level of evaluation.

Level of evaluation	*1991*		*1992*		*1993*		*Total*	
	No on trial	*% selected*	*No on trial*	*% selected*	*No on trial*	*% selected*	*No on trial*	*% selected*
4*x* x 2*x* = TD								
1st	321	38	42	38	65	64	428	42
2nd	–	–	121	53	16	56	137	53
3rd	–	–	–	–	64	41	64	41
2*x* x 4*x* = DT								
1st	47	13	1	0	0	–	48	13
2nd	–	–	6	67	0	–	6	67
3rd	–	–	–	–	4	50	4	50
2*x* x 2*x* = DD								
1st	40	52	0	–	2	50	42	52
2nd	–	–	21	38	0	–	21	38
3rd	–	–	–	–	7	57	7	57
1st							518	40
2nd							164	52
3rd							75	44

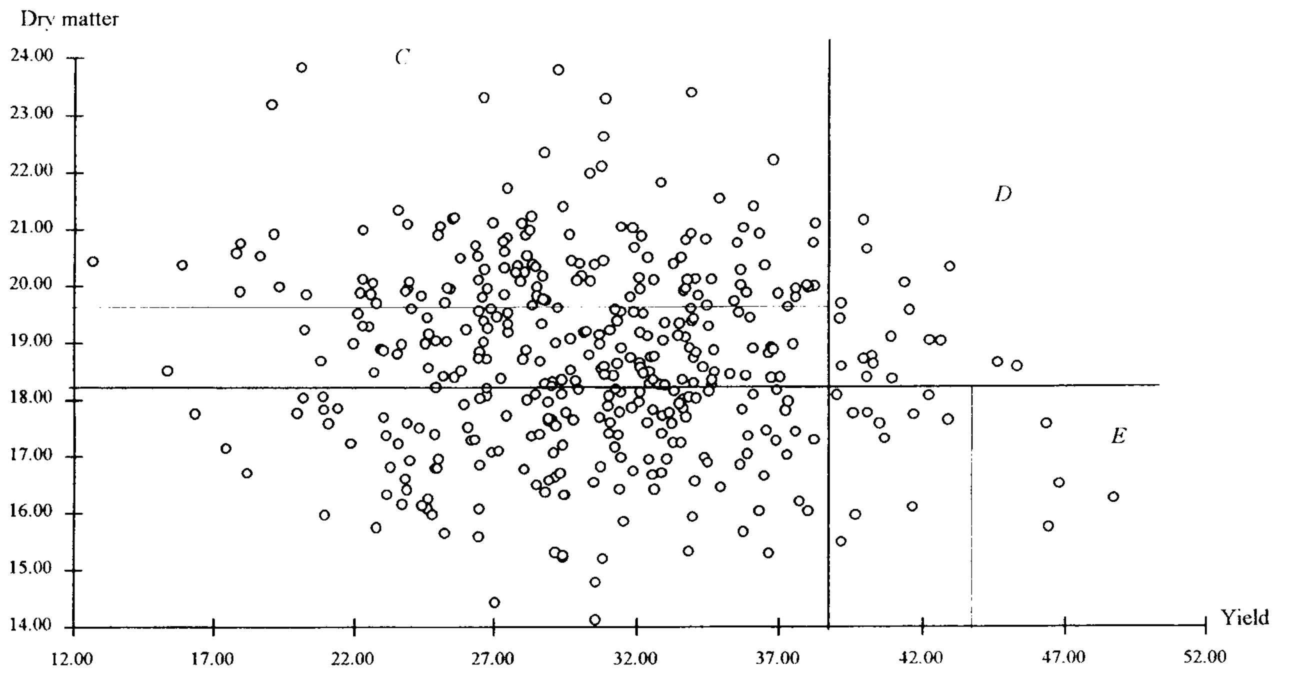

Fig 3. Selection plan in 1991 for marketable yield and dry matter content (see fig 2 for explanation of thresholds).

Table V. Values of characters measured in each year of screening for the control varieties Bintje and Claustar, each series of clones on first screening, clones selected in these series and clones in second or third screening in 1993.

	Total yield (kg)	*Marketable yield (kg)*	*Total No of tubers*	*No of marketable tubers*	*Mean tuber weight (g)*	*Dry matter (%)*	*Chips*	*Blackening*	*Sloughing*	*Absorbed energy (mJ)*
1991										
Bintje										
Mean	35.79	34.48	364	283	122	19.79				
Claustar										
Mean	44.43	43.20	297	257	168	16.85				
Clones 1st screening										
Mean	32.13	30.48	374	278	112	18.72				
sd	5.67	5.86	86	51	26	1.66				
Minimum	15.45	12.68	123	104	51	14.12				
Maximum	49.12	48.72	749	438	255	23.84				
Clones selected										
Mean	33.09	31.40	377	283	114	20.15				
sd	6.68	7.07	85	50	33	1.45				
Minimum	15.45	12.68	123	104	51	15.66				
Maximum	49.12	48.72	749	426	255	23.84				
1992										
Bintje										
Mean	21.60	20.08	312	244	82	22.67	30			
Claustar										
Mean	28.80	28.45	216	205	139	19.25	15			
Clones 1st screening										
Mean	25.02	23.33	292	238	102	20.38	23.89			
sd	3.50	5.95	85	54	25	1.83	7.92			
Minimum	15.30	17.33	145	127	47	16.99	0			
Maximum	37.24	34.89	529	391	167	24.01	30			
Clones selected										
Mean	24.31	24.96	246	213	121	20.78	24.44			
sd	4.13	3.26	74	51	25	2.23	6.94			
Minimum	17.65	18.83	145	127	80	17.75	15			
Maximum	31.41	30.68	369	296	167	24.01	30			
1993										
Bintje										
Mean	28.94	27.44	354	284	97	18.78	30	2.67	1	640
Claustar										
Mean	36.77	35.92	293	265	135	17.01	15	0	2	648
Clones 1st screening										
Mean	32.87	31.04	348	285	113	17.51	17.85	1	0.83	649
sd	4.30	4.85	75	56	27	1.33	9.56	1.12	0.89	21
Minimum	22.64	21.97	192	174	62	14.09	0	0	0	616
Maximum	45.18	43.21	548	399	201	20.24	30	3	2	711
Clones selected										
Mean	34.64	33.12	342	279	122	17.75	17.57	1.07	0.81	647
sd	4.39	4.37	86	60	26	1.39	9.45	1.14	0.88	20
Minimum	24.23	23.77	192	174	78	14.74	0	0	0	626
Maximum	45.18	43.21	548	399	201	20.24	30	3	2	689
Clones 2nd and 3rd screening										
Mean	32.60	31.20	326	264	124	19.18	20.61	0.86	0.96	661
sd	5.24	5.40	94	60	33	1.90	9.05	1.13	0.78	31
Minimum	17.44	17.09	151	133	57	14.64	0	0	0	599
Maximum	45.58	43.76	698	403	231	24.45	30	3	2	746

Numbers of clones involved are given in table IV.

Latin squares which have a more square surface on the field and have a higher number of degrees of freedom.

The agronomic evaluation was first applied on the fourth year of selection in the field (fifth year including seedling stage). On average, 4.32% of the seedling genotypes were still represented. This was low but enabled us to discard all clones with real tuber defects and did not greatly alter variability for other traits.

The production of 2*n* gametes was frequent in diploid potato populations. However, not many clones could produce enough true seeds by sexual polyploidization (result not published), and this was a serious bottleneek for the diploid scheme. The type of 2*n* gametes present in the diploid parents was not checked, as our purpose was to bring as many diploid genotypes as possible to the tetraploid level, and then to select 4*x* clones and not to compare progenies or genetic value of the parents.

It would have been interesting to compare results of TD, DT and DD. However, this was not possible because the study was not designed for this purpose: the genetic backgrounds of the various groups were different, the size of each group was not equal, and the tested clones only represented a part of the whole variability.

The selected TDO are now being incorporated into a buffer tetraploid population, and are being used further to introduce new variability into the breeding programmes at the tetraploid level. The value of such TDO clones will be higher when specific traits such as resistance are introduced.

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