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Inbreeding in cultivated diploid potatoes*

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Zusammenfassung, Résumé p. 81

Summary

The effects of inbreeding in cultivated diploid potatoes were studied by using self-fertile hybrids from crosses between Group Phureja and Group Stenotomum and haploids of Group Tuberosum. S_1, S_2 and S_3 progenies usually exhibited decreased performance and vigour with increased inbreeding. In most families the inbreeding depression seemed to coincide with a curve calculated on the basis of the expected loss of heterozygosity in a diploid organism. The performance of some progenies deviated markedly from expectations apparently because a non-random sample of parents contributed to later generations. Many inbred genotypes were lost owing to poor seedling vigour or tuberization. This indicated the presence of many harmful recessive genes. The rapid increase in homozygosity following selfing at the diploid level provides a means for developing homozygous clones with a potential for use in future genetic investigations.

Introduction

The success of hybridization between inbred lines in maize has led to many similar investigations with other crops. Several workers have reported inbreeding studies in cultivated tetraploid potatoes (Engel, 1957; Feistritzer, 1952, Gowen, 1956; Krantz, 1924, 1946; Krantz and Hutchins, 1929; Mullin and Lauer, 1966; Rudorf, 1958). Such studies have not been reported in cultivated diploid potatoes, probably because most of the diploid *Solanum* species are self-incompatible (Cipar et al., 1964). Research in this area is now possible as a result of studies of haploids of the cultivated tetraploid potato (*S. tuberosum L.* Group Tuberosum). Crosses between cultivated diploid species and male-fertile Tuberosum haploids produce vigourous, highly fertile progeny. Most of these 24-chromosome hybrids are self-incompatible, but crosses involving haploids from an inbred Minnesota seedling, *Minn. 20-20-34*, (primarily *US-W4*) were found to be self-fertile (Smiley, 1963; Cipar, 1964).

This paper describes the effect of inbreeding on populations derived from diploid-haploid hybrids. An inbreeding study with a genetic base of diploid hybrids, has several advantages: 1) since the tetraploid varieties and self-incompatible diploid species may have several recessive genes not normally expressed, these hybrids should

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be an extremely fertile source of unexplored genetic variability (Hougas and Peloquin, 1962); 2) the rate of progress towards homozygosity following selfing is much faster with diploids than with autotetraploids. The number of generations needed to reduce heterozygosity by 50 per cent by inbreeding is 1 in diploids and 3.8 in autotetraploids (Bartlett and Haldane, 1934); 3) stocks homozygous for marker genes of potential value for future genetic investigations can be obtained much faster; 4) the segregation ratios obtained for progenies from selfed seed would be much easier to analyze with a disomic inheritance pattern. Progeny analysis based on selfing can be a powerful tool for evaluating potential parents for a crossing programme (Feistritzer, 1952; Krantz and Hutchins, 1929).

Materials and methods

The experiments were conducted at the Potato Introduction Station, Sturgeon Bay, Wisconsin. The initial genetic base consisted of the following hybrid families:
US-W 5309 (*Phu PI 195191* × *US-W4*)
US-W 5314 (*Phu PI 225708.1* × *US-W4*)
US-W 5315 (*Phu PI 225675.1* × *US-W4*)
US-W 5328 (*Stn PI 230513.1* × *US-W4*)

In each generation, plants were self-pollinated and the seed produced by self-fertile plants bulked to produce subsequent generations. Observations were made on populations grown from true seed and from tubers. Families grown from true seed were started in the greenhouse and transplanted to the field. Two replicates of seedling populations were obtained by dividing a bulked population of seed into 2 equal lots. All plants producing tubers were saved for evaluation in tuber plantings. Replicated trials were planted in the field in 2 years.

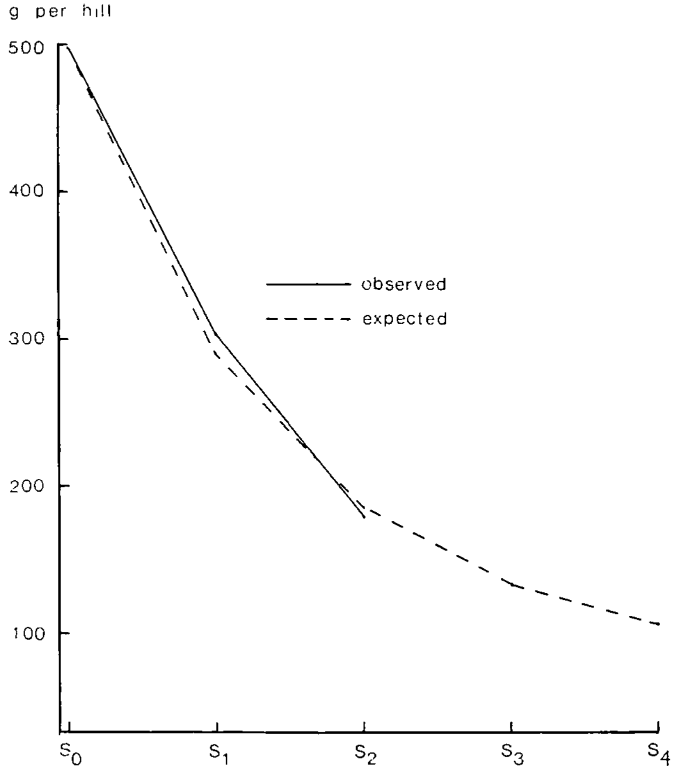
The following characteristics were measured:

1. Plant height – in cm when the plants had reached maximum height.
2. Vigour index – based on total amount of foliage. Individual plants were rated on a scale from 1 (very weak or small) to 5 (very vigourous).
3. Number of tubers per hill.
4. Tuber weight – g per hill.
5. Self-, pollen-, and ovule-fertility. The fertility data were obtained by using the decapitation technique (Peloquin and Hougas, 1959). Tests were conducted on all replicates planted from tubers in 1968 (Table 3). For each inbred clone, 3 stems with 4 buds each were collected at random from a large population of Phureja plants, and these 12 flowers were then used as females to test the pollen fertility of the inbred population. Up to 2 stems, also with 4 buds each, were cut from each flowering clone of the inbred populations. On each stem three flowers were used to test the self-fertility, and one flower was emasculated and pollinated with a mixture of pollen from the Phureja population to measure the ovule fertility. A total of 3651 pollinations were made; of these 935 were made to measure self-fertility, 2375 to measure pollen fertility and 341 to measure ovule fertility.

Results

Inbreeding depression was expressed by all measured characters. When averaged over the 4 families, the inbreeding depression generally followed the rate expected based on reduction of heterozygosity. In the case of tuber weight per hill for the populations grown from tubers in 1968, it was possible to calculate a curve which agreed very well with the observed data (Fig. 1). Considerable variation in response to inbreeding existed between families (Table 1). Family *US-W 5328* exhibited inbreeding depression at each generation of inbreeding. Family *US-W 5309* had a sharp depression from the

Fig. 1. Average tuber weight in g per hill (1968).



g per hill – *g pro Staude – gr/touffe*
generation – *Generation – génération*
observed – *festgestellt – observé*
expected – *erwartet – attendu*

Abb. 1. Mittleres Knollengewicht in g/pro Staude (1968).
Fig. 1. Poids moyens de tubercules en gr/touffe (1968).

Table 1. Effect of inbreeding on four diploid potato families.

Family[1]	Number of clones[2]			Plant height[3] (cm)			Vigour index[4]			Tubers/hill[5]			Tuber weight g/hill[6]		
	S_0	S_1	S_2	S_0	S_1	S_2	S_0	S_1	S_2	S_0	S_1	S_2	S_0	S_1	S_2
First clonal generation[7]															
US-W 5309	12	16	16	43	25	27	3.5	2.3	2.5	21	16	15	563	248	269
US-W 5328	9	12	8	41	27	17	3.6	2.4	1.6	19	15	8	390	425	167
US-W 5314	0	12	11		27	23		2.4	2.2		13	7		287	88
US-W 5315	0	10	9		25	29		2.6	2.7		20	21		297	415
Total	21	50	44												
Weighted average[8]				42	26	25	3.5	2.4	2.2	20	16	14	499	304	181
% of S_0[9]				100	62	60	100	69	63	100	80	70	100	61	36
Second or later clonal generations[10]															
US-W 5309	12	10	11	31	23	31	3.6	2.8	3.7	10	14	12	198	165	217
US-W 5328	7	11	4	37	28	14	4.0	3.3	2.0	20	13	5	370	330	13
US-W 5314	0	10	4		22	22		2.7	2.6		13	13		100	95
US-W 5315	0	9	7		20	25		2.5	3.5		13	14		202	237
Total	19	40	26												
Weighted average[8]				33	24	25	3.7	2.9	3.2	14	13	12	260	211	175
% of S_0[9]				100	73	76	100	78	86	100	93	86	100	81	67

[1] *Familie – Familles*
[2] *Anzahl Klone – Nombre de clones,*
[3] *Pflanzenhöhe – hauteur des plantes*
[4] *Frohwüchsigkeit (Index) – Index de vigueur*
[5] *Knollen/Staude – Tubercules/touffe*
[6] *Knollengewicht g/Staude – Poids (gr) de tub. par touffe*
[7] *Erste Klongeneration – première génération clonale*
[8] *Gewogenes Mittel – Poids moyen*
[9] *in % von S_0 – % de S_0*
[10] *Zweite oder spätere Klongenerationen – Seconde ou suivantes générations clonales*

Tabelle 1. Einfluss der Inzucht auf vier diploide Kartoffelfamilien.
Tableau 1. Effet de l'autofécondation sur quatre familles de Pomme de terre diploïdes.

S_0 to the S_1, but the subsequent S_2 generation was not depressed. The performance of families *US-W 5314* and *US-W 5315*, respectively, was slightly lower and slightly higher in the S_2 than in the S_1 (Table 1).

The inbreeding depression of populations obtained by clonal reproduction was nearly always less than in the asexual parent population (Tables 1 and 2). In all cases the asexual progenies contained fewer genotypes than their parent populations, because of lack of tuberization in the parent populations. Clones planted from tubers exhibited reduced tuberization that increased with each subsequent level of inbreeding (Table 3).

There was a severe inbreeding depression from S_0 to S_1 for all characters for all

Table 2. Effect of inbreeding on potato populations grown from true seed and the first clonal generation

Character[1]	Seedling populations (1968)[2]				First clonal generation (1969)[3]			
	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3
Number of plants[4]	29	163	184	163	11	41	48	35
Plant height (cm)[5]	25	16	16	15	46	21	20	20
% of S_0[6]	100	64	64	59	100	46	43	42
Vigour index[7]	5	2	3	3	5	3	3	3
% of S_0[6]	100	51	57	57	100	60	60	60
Tubers/hill[8]	10	6	5	5	23	16	20	16
% of S_0[6]	100	60	50	50	100	70	87	70
Tuber weight (g/hill)[9]	61	20	16	14	426	236	234	193
% of S_0[6]	100	33	26	23	100	55	55	45
% tuberizing[10]	69	81	80	71	97	93	94	83
% with $\geq$ 1 viable tubers after storage[11]	62	70	72	63				
% with $\geq$ 4 viable tubers after storage[12]	38	33	32	25				

[1] *Eigenschaft – Caractère*
[2] *Sämlingspopulationen (1968) – Populations de plantules (1968)*
[3] *Erste Klongeneration (1969) – Première génération clonale (1969)*
[4] *Anzahl pflanzen – Nombre de plantes*
[5] *Pflanzenhöhe (cm) – Hauteur des plantes (cm)*
[6] *in % von S_0 – % de S_0*
[7] *Frohwüchsigkeit, Index – Index de vigueur*
[8] *Knollen/Staude – Tub./touffe*
[9] *Knollengewicht (g/Staude) – Poids des tub. (gr/touffe)*
[10] *% mit Knollenansatz – % de tubérisation*
[11] *% mit $\geq$ 1 lebensfähiger Knolle nach der Lagerung – % avec $\geq$ 1 tubercule viable après conservation*
[12] *% mit $\geq$ 4 lebensfähigen Knollen nach der Lagerung – % avec $\geq$ 4 tubercules viables après conservation*

Tabelle 2. Einfluss der Inzucht auf Kartoffelpopulationen, entstanden aus Samen und der ersten Klongeneration.
Tableau 2. Effet de l'autofécondation sur des populations de pomme de terre issues de vraies semences et sur la première génération clonale.

families when grown from true seed. There was little if any depression in the subsequent S_2 and S_3 generations. These populations tuberized fairly well in the field even in the advanced generations of inbreeding. Most of these tubers were very small, however, and were not viable the following spring after standard winter storage conditions (Table 2).

The per cent of plants that flowered, the per cent of fertile flowering plants, and the level of fertility decreased very sharply from the S_0 to the S_1 but not from S_1 to S_2 (Table 4). The self-fertility was much lower than either the pollen or ovule fertility at all levels of inbreeding.

Table 3. Effect of inbreeding on asexual reproduction.

Year[1]	Number of clones planted[2]		
	S_0	S_1	S_2
1968	21	50	44
1969	19	40	26
Per cent replanted in 1969[3]	90	80	59

[1] *Jahr – Année*
[2] *Anzahl ausgepflanzter Klone – Nombre de clones plantés*
[3] *% 1969 nachgebauter Klone – Pourcents replantés en 1969*

Tabelle 3. Einfluss der Inzucht auf die ungeschlechtliche Vermehrung.
Tableau 3. Effet de l'autofécondation sur la reproduction assexuée.

Table 4. Effect of inbreeding on flowering and fertility.

Level of inbreeding[1]	Clones planted[2]	Per cent stand[3]	Per cent flowering[4]	Fertility in per cent of flowering clones[5]			Seeds/fruit for fertile plants[6]		
				Self-[7]	Pollen-[8]	Ovule-[9]	Self-[7]	Pollen-[8]	Ovule-[9]
S_0	21	95	100	47	85	86	12	54	76
S_1	50	91	54	16	34	23	9	36	34
S_2	44	74	54	16	41	47	6	38	30

[1] *Inzuchtgrad – Degré de consanguinité*
[2] *Anzahl gepflanzter Klone – Clones plantés*
[3] *Prozent Pflanzenentwicklung – Situation en %*
[4] *Prozent Blühzustand – % de floraison*
[5] *Fertilität in % der blühenden Klone – Fertilité en % des clones fleurissant*
[6] *Samen/Frucht für fruchtbare Pflanzen – Semences par fruit chez les plantes fertiles*
[7] *Selbst – Auto*
[8] *Pollen- – Pollen-*
[9] *Eizellen – Ovule*

Tabelle 4. Einfluss der Inzucht auf den Blühzustand und die Fruchtbarkeit.
Tableau 4. Effet de l'autofécondation sur la floraison et la fertilité.

Discussion

Generally the average performance of the 4 families decreased with each subsequent level of inbreeding. For some characters, the inbreeding depression coincided with a curve calculated on the basis of heterozygosity in a diploid organism (Fig. 1 and Table 1). Such a response is expected of a crop that is normally highly heterozygous, cross-pollinated and vegetatively propagated. Upon inbreeding tetraploids, Krantz (1946) obtained an S_2 that yielded 82% of the S_0, whereas in this experiment the first clonal generation S_2 yielded only 36% of the S_0 (Table 1). The difference can be attributed to the more rapid increase in homozygosity at the diploid level. The 4 families responded differently to inbreeding. The fluctuations in response were partly due to reproductive difficulties (both sexual and asexual) which increase with inbreeding. The genetic differences between the original parent populations (S_0) could also have contributed to differences in response to inbreeding. This was observed at the tetraploid level by Krantz and Hutchins (1929).

Attempts to obtain each subsequent level of inbreeding from a representative sample of parents at the preceding level were not always successful. Only the more vigorous plants flowered, and only a portion of these were self-fertile in the advanced generations of inbreeding (Table 4). A selection for vigour in the sexual cycle has also been observed upon inbreeding at the tetraploid level (Krantz, 1946; Krantz and Hutchins, 1929). The self-fertility was considerably lower than either pollen or ovule fertility for all levels of inbreeding when expressed either as per cent of flowering clones or as seeds per fruit. A reduction in seed set for self-, pollen- and ovule-fertility could be demonstrated with each subsequent level of inbreeding (Table 4). A considerably higher seed set upon selfing the S_0 of similar material has been reported (Hollenback, 1966; Smiley, 1963). In our experiment, however, special efforts were made to obtain selfed seed from the weaker clones as well as from the more vigourous ones. This procedure was necessary to obtain a sample of selfed seed as nearly random as possible, but probably contributed to a lower self-fertility level in the S_0 than reported by others. Rudorf (1958) reported similar reproductive difficulties upon inbreeding tetraploids. He could not obtain the S_3 in most of his inbred lines due to their lack of vigour, and to virus infection and reduced fertility.

Approximately 45% of the genotypes were lost between the time of planting the seed to the transplanting stage. Similar losses were reported by Engel (1957). For several genotypes we were unable, due to lack of tuberization, to obtain the second clonal generation. When the performance of the first clonal generations was compared with the asexual progenies, the depression in relation to the respective S_0's was smaller for most progenies than for their respective asexual parental populations. (Tables 1 and 2). This can probably be attributed in part to the difficulties with asexual reproduction. Many plants that could be classified as 'tuberizing' in the seedling year, nevertheless only produced small immature tubers which were not viable the following spring after standard storage conditions. The per cent of seedlings with 4 or more viable tubers the following spring was considerably lower in the S_3 than in the S_0, although the per cent of plants classified as 'tuberizing' was approximately the same for the S_0 and S_3 (Table 2). The problems with asexual reproduction indicate that harmful recessive genes may have been uncovered, the expression of which is delayed until after the first clonal generation, or until an unfavourable reaction between the environment and the weaker genotypes occurs. The genotypes in which lethal or semi-lethal genes are expressed are automatically excluded from contributing to the subsequent generation, which in turn affects the rate of inbreeding. In spite of these problems in reproduction, several fairly vigourous S_5 lines have now been obtained. Many of these lines exhibit a high degree of uniformity in leaf type, tuber shape and patterns of pigmentation. Other S_5 lines are still segregating for these same characters.

It appears, therefore, that it is possible to obtain homozygous clones for future genetic studies on the diploid level. Assuming no selection for heterozygosity, the diploid S_5 generation is about 97% homozygous. In comparison, the autotetraploid S_5 generation, assuming random chromosome segregation, would only be 53% homozygous (Bartlett and Haldane, 1934). The unavoidable selection for vigour during reproduction, although kept to a minimum, probably resulted to a certain extent in some selection for heterozygosity as well. However, the diploid S_5 generation probably represents the greatest degree of inbreeding ever imposed upon potatoes.

Inbreeding by selfing imposes selection for self-fertility and, although such lines have not yet been detected, lines homozygous for this trait might be expected. They would be very useful in investigating the genetics of self-fertility. Linkage relations with the gene(s) for self-fertility will have special interest. Simmonds (1966) reported a case of linkage of a harmful recessive gene to the S-locus in potato. If the gene(s) for self-fertility are linked to recessive lethals, it may be difficult to develop true breeding self-fertile clones.

The rapid decline of vigour upon inbreeding suggests that hybrid vigour may be obtained when two inbred clones with a high combining ability are crossed. Considering the success with hybrid vigour in other crops, this area certainly warrants further investigation in potatoes, especially on the diploid level where advanced inbred lines can be obtained in a relatively short time. A broader genetic base will probably be necessary to develop more diverse inbred lines that can be used as parents to produce maximum hybrid vigour.

Zusammenfassung

Inzucht bei kultivierten diploiden Kartoffeln

Inzucht bei kultivierten diploiden Kartoffeln wurde möglich, nachdem man herausgefunden hatte, dass Kreuzungen zwischen kultivierten diploiden Arten und gewissen Haploiden von *Solanum tuberosum* in hohem Masse selbstfertil sind. Die ursprüngliche genetische Basis dieses Versuches bestand aus 4 Familien, die durch Kreuzungen zwischen der Gruppe Phureja und der Gruppe Stenotomum mit der Gruppe Tuberosum haploid *US-W 4* erzielt wurden. Bei einer Anzahl der untersuchten Eigenschaften stimmte die durchschnittliche Inzuchtdepression der 4 Familien mit einer Kurve überein, die auf der Basis der Heterozygotie in einem diploiden Organismus (Tabellen 1, 2 und Abb. 1) berechnet wurde. Die vier Familien reagierten unterschiedlich auf die Einkreuzung (Tabelle 1). Dies kann teilweise auf genetische Unterschiede zwischen den ursprünglichen Elternpopulationen (S_0) und auf eine Auslese auf Frohwüchsigkeit sowohl im geschlechtlichen als auch im ungeschlechtlichen Vermehrungszyklus zurückgeführt werden. Nur die kräftigeren Pflanzen blühten, und nur ein kleiner Teil davon war in den fortgeschrittenen Inzuchtgenerationen selbstfertil (Tabelle 4). Dies zeigt, dass Allele für Selbstunverträglichkeit in den Populationen noch vorhanden sind. Der niedrigere Grad der Selbstfertilität, ausgedrückt in Samen pro Frucht, weist beim Vergleich mit der Pollen- und der Eizellenfertilität darauf hin, dass rezessive lethale Gene vorhanden sind. Fortgeschrittene Inzuchtgenerationen wiesen eine abnehmende Knollenbildung auf (Tabelle 3). Beim Vergleich der Leistung der ersten Klongenerationen mit jener der ungeschlechtlichen Nachkommenschaften war die Depression in bezug auf die entsprechenden S_0's bei den meisten Nachkommenschaften kleiner als bei ihren entsprechenden ungeschlechtlichen Elternpopulationen (Tabellen 1 und 2). Es wurden einige kräftige S_5-Linien er-

zielt, manche von ihnen besitzen einen hohen Grad von Einheitlichkeit. Die rasche Abnahme der Frohwüchsigkeit nach der Einkreuzung deutet darauf hin, dass ein Heterosiseffekt bei Kreuzung fortgeschrittener Inzuchtklone erreicht werden könnte. Da Inzucht durch Selbstung eine Auslese auf Selbstfertilität erfordert, könnte dieses Vorgehen einige homozygote, selbstfertile Linien hervorbringen, was für eine Untersuchung der Genetik der Selbstfertilität sehr nützlich wäre.

Résumé

L'autofécondation dans les pommes de terre cultivées diploïdes

L'autofécondation chez les pommes de terre cultivées diploïdes devint possible quand on découvrit que des croisements entre espèces cultivées diploïdes et certains haploïdes de *Solanum tuberosum* étaient hautement auto-fertiles. La base génétique initiale de la présente étude comprend 4 familles issues de croisements entre groupe Phureja et groupe Stenotomum avec le haploïde *US-W4* du groupe Tuberosum. Pour un certain nombre de caractères, la dépression moyenne de consanguinité des 4 familles coïncide avec une courbe calculée sur la base de l'hétérozygotie dans un organisme diploïde (Tableaux 1, 2 et Fig. 1). Les 4 familles réagissaient différemment à l'autofécondation (Tableau 1). Ceci peut partiellement être attribué à des différences génétiques entre les populations parentales originales (S_O) et à une sélection pour la vigueur dans les cycles de reproduction à la fois sexuelle et asexuelle. Seules les plantes les plus vigoureuses fleurissaient, et seule une petite partie de celles-ci étaient auto-fertiles dans les générations successives autofécondées (Tableau 4). Ceci indique que les allèles d'autoincompatibilité sont toujours présents dans les populations. Le niveau plus faible d'auto-fertilité exprimée par le nombre de graines par fruit, quand on la compare à la fertilité du pollen et de l'ovule fait supposer que des gènes létaux récessifs sont présents. Les générations autofécondées successives montrent une tubérisation décroissante (Tableau 3). Quand on compare les performances des premières générations clonales avec les descendances assexuées, la dépression, comparée aux S_O respectifs, est plus faible chez la plupart des descendances que chez les populations parentales assexuées respectives (Tableaux 1 et 2). Plusieurs lignées S_5 bien vigoureuses ont été obtenues, plusieurs de celles-ci montrant un haut degré d'uniformité. Le déclin rapide dans la vigueur après autofécondation suggère qu'on peut obtenir des hybrides vigoureux de croisements entre clones précédemment autofécondés. Puisque la consanguinité par autofécondation impose une sélection pour l'autofertilité, on peut de la sorte produire quelques lignées homozygotes auto-fertiles qui pourraient être utiles pour une recherche sur la génétique de l'autofertilité.

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