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Cytoplasmic evaluations during substitution backcrossing in *Solanum**

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Zusammenfassung, Résumé p. 317

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Summary

Sterility-resistant cytoplasmic factors of *Solanum tuberosum* ssp. *andigena* (Juz. & Buk.) Hawkes and of *Solanum phureja* (Juz. & Buk.) were combined with chromosomal genes of *S. tuberosum* ssp. *tuberosum*. Eleven morphological characters of reciprocal F_1 and BC_1 progenies were monitored to evaluate rate of progression towards characteristics occurring in the recurrent ssp. *tuberosum* parent. Female and male fertilities of F_1 and BC_1 populations were also evaluated.

Cytoplasmic factors did not influence morphological parameters consistently, except those relating directly to fertility. Differences between reciprocal progeny depended more upon the genes of individual parents used in crosses than on cytoplasm source. No consistent reciprocal differences occurred in tuber characters and those differences which arose seem to reflect a maternal rather than a cytoplasmic influence. F_1 and BC_1 progenies containing the sterility-resistant cytoplasmic factors of ssp. *andigena* or of *S. phureja* had higher fertility than their respective reciprocal progenies with cytoplasm of ssp. *tuberosum*.

Introduction

Cytoplasmic sterilities are very common in the genus *Solanum* and as a result of their action many strains of cultivated potatoes *(Solanum tuberosum* L. ssp. *tuberosum)* are sterile and cannot be used in plant breeding programs (Abdalla & Ramanna, 1971; Clark, 1927; Grun et al., 1977; Grun, 1979; Grun & Staub, 1981; Hoopes et al., 1980; Koopmans, 1951, 1952, 1955; Mullin & Lauer, 1966; Salaman & Lesley, 1922; Sanford & Hanneman, 1979). It has been established that the cultivated potato contains cytoplasmic factors which are inherited through the female parent and interact with chromosomal genes inherited through both parents to produce at least ten different sorts of abnormalities, all related to sterility. These sterilities occur when the cytoplasm of the cultivated potato is combined with dominant chromosomal genes that occur in other species such as *S. phureja, S. stenotomum, S. vernei,* and *S. tuberosum* ssp. *andigena* (Grun, 1974; 1979; Sanford & Hanneman, 1979). This fact has led to the interpretation that the sterilities of the cultivated potato may be cytoplasmic in nature and reflect the presence, within ssp. *tuberosum,* of the nuclear genes to which its cytoplasm is sensitive

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(Grun & Staub, 1981).

Thus, hybrids between commercial potatoes and wild species, when produced as part of the process of potato improvement, are often sterile. This poses problems for the potato breeders (Mullin & Lauer, 1966), because many of these wild and cultivated species contain useful genes for disease, insect, drought and could resistance. Therefore, a project was initiated to replace the cytoplasmic factors of northern hemisphere cultivars of ssp. *tuberosum* with factors which lead to fertility. This process involved combining sterility-resistant cytoplasm of two potato species from Andean regions of South America (*Solanum tuberosum* L. ssp. *andigena* (Juz. & Buk.) Hawkes and *Solanum phureja* (Juz. & Buk.)) with chromosomal genes of ssp. *tuberosum*. A substitution backcrossing program has been initiated to restore acceptable commercial quality while retaining the resistant cytoplasm.

This communication describes the effects of the insertion of chromosomal genes of *Solanum tuberosum* ssp. *tuberosum* into the cytoplasmic background of ssp. *andigena* and *Solanum phureja* in reciprocal F_1 and BC_1 populations. A number of morphological and fertility parameters were monitored to determine the effect of cytoplasmic source on these parameters and the rate of progression, during backcrossing, towards characteristics occurring in the recurrent ssp. *tuberosum* parent.

Materials and methods

The *S. tuberosum* ssp. *tuberosum* cultivars (T), North American adapted ssp. *andigena* clones (A) and a *S. phureja* × *S. chacoense* hybrid, clone JV-2, (PC) which were used as parents in this project are listed in Table 1. Letters in brackets, i.e. [T], [A], and [P], are used to symbolize cytoplasmic backgrounds of ssp. *tuberosum*, ssp. *andigena*, and *S. phureja*, respectively. Hand pollinations were used after bud emasculation, and care was taken to protect crossed flowers from foreign pollen (Grun, 1961).

Initial crosses of parental material produced seven sets of reciprocal F_1 progeny groups: four sets in ssp. *andigena* and three sets in *phureja* cytoplasmic backgrounds. The ssp. *andigena* × ssp. *tuberosum* and *(S. phureja* × *S. chacoense)* × ssp. *tuberosum* crosses represented the initial insertion of ssp. *tuberosum* chromosomal genes into the resistant cytoplasmic backgrounds. Reciprocal F_1 progeny were raised in parallel rows as single hill plants spaced 1.50 m apart. Tubers from fifty F_1 plants, taken at random, were harvested from each of the reciprocal pairs (100 plants per reciprocal pair). Tubers of the F_1 progeny were arranged as a randomized complete block design with a split-plot arrangement of treatments. There were seven blocks; the main plots were the two cytoplasm and the subplots were the seven reciprocal sets with fifty individuals in each reciprocal lot. Tubers of these reciprocal F_1 progeny were harvested, and the number and weight of the tubers were recorded.

Reciprocal BC_1 crosses to the recurrent ssp. *tuberosum* parent were raised in a field nursery the following year as single hill plants spaced 1.50 m apart. Plants were set in a randomized complete block design with a split-plot arrangement of treatments. There were four blocks; the main plots were the two cytoplasms and the subplots were thirteen reciprocal families. Ten reciprocal sets were in *andigena* cytoplasmic background and three sets in a *phureja* cytoplasmic background. The primary consideration of this study was the comparison of reciprocal progenies. Therefore, in order to grow an adequate

Table I. Identification and source of *Solanum tuberosum* parental material used in the production of reciprocal F_1 and BC_1 populations.

Clone identification[1]	Clonal source[2]*	Taxonomic classification[3]	Experimental designation[4]
Norchip	A, C	ssp. *tuberosum*	T_1
Hudson	A, B	ssp. *tuberosum*	T_2
Red Pontiac	A, C	ssp. *tuberosum*	T_3
Superior	A, C	ssp. *tuberosum*	T_4
Kennebec	A, C	ssp. *tuberosum*	T_5
Katahdin	A, C	ssp. *tuberosum*	T_6
4NJV2	D	Induced tetraploid of Interspecific hybrid *S. phureja* × *S. chacoense*	PC
R85-4	B	ssp. *andigena*	A_1
R133-10	B	ssp. *andigena*	A_2
R247-1	B	ssp. *andigena*	A_3

* A = Dr. Raymon Webb, Beltsville, MD; B = Dr. Robert Plaisted, Ithaca, N.Y.; C = Dr. Richard Cole, University Park, PA; D = Part of the potato genetics project, The Pennsylvania State University - *Teil des Kartoffelgenetikprojektes* *Provenance du projet génétique sur la pomme de terre.*

[1] *Klon-Kennzeichnung - Identification des clônes;* [2] *Klon-Herkunft - Origine des clônes;* [3] *Taxonomische Eingruppierung - Classe taxonomique;*[4] *Experimentelle Bezeichnung - Désignation expérimentale;*[5] *Induziert Tetraploid von der interspezifischen Hybride (aus) S. phureja* × *S. chacoense - Hybride interspécifique tétraploïde issu du croisement S. phureja* × *S. chacoense*

Tabelle I. Kennzeichnung und Herkunft des Elternmaterials von *Solanum tuberosum*, das zur Produktion der reziproken F_1- und BC_1-Populationen verwendet wurde.
Tableau I. Identification et origine des *Solanum tuberosum* parentaux utilisés dans la production des populations réciproques de F_1 et BC_1.

sample of each reciprocal pair while staying within space limitations, it was necessary to limit the total number of backcross progeny to thirteen. Fifteen ssp. *tuberosum* and ten ssp. *andigena* clones were used as standards for measuring rate of progression in T × A reciprocal crosses. Clones were set in separate plots and arranged in a randomized complete block design with three replications.

Notes on above-ground and/or below-ground phenotypic characters were taken in all trials to determine effects of cytoplasmic source and rate of progression towards a recurrent parent. The morphological characters were chosen which separated ssp. *andigena* from ssp. *tuberosum* (Correll, 1962; Hawkes, 1956; Salaman, 1926; Simmonds, 1964). The phenotypic parameters monitored were: (1) largest adjacent leaflet width, length and area; (2) terminal leaflet length and area; (3) leaf angle; (4) number of interjected leaflets; (5) petiolule length; (6) style thickness; and (7) total tuber weight, number and average tuber weight, and tuber eye depth. Measurements of any one character were made at the same time but different characters were scored at different times. For example, leaflet dimensions were recorded earlier in the growing season than leaflet are measurements. All leaflet measurements were taken on the third leaf (usually the first fully expanded) from a terminal shoot apex when plants were at full maturity. Leaflet area was measured by passing three leaflet samples per plant through a stationary

leaf area meter (Li-Cor Instruments, Inc., Lincoln, Nebraska) and calculating an average leaflet area value. All measurements were taken on BC_1 families. Measurements of petiolule and style thickness were not recorded for 1978 F_1 populations. Tuber weight and number were the only parameters recorded during the 1978 greenhouse trial. Tubers in all trials were hand-harvested and stored at approximately 15 °C. Measurements were taken within 60 days after harvest.

Data from 1978 F_1 field trials were analysed by a paired t-test, and an analysis of variance was performed on data from 1978 F_1 greenhouse and 1979 BC_1 field progenies. The variances of BC_1 sibling lots were found to be homogeneous for above-ground and below-ground characteristics (Bartlett's test for homogeneity) and sibling lots were grouped in five BC_1 families. Variances of reciprocal F_1, $T \times A$ and $T \times PC$ families for above-ground characteristics were homogeneous. Means for 1978 F_1 greenhouse and 1979 BC_1 progenies were also homogeneous. Means for 1978 F_1 greenhouse and 1979 BC_1 progenies were compared by Duncan's least significant difference test at $P < 0.05$ and $P < 0.01$.

Female and male fertility of F_1 and BC_1 populations was evaluated at the end of the growing season by recording relative amount of berry set and anther indehiscence, anther width and length, anther color, and by cytological observations of anther smears. Berry set classes ranged from 0–2, where 0 signifies no berry set, 1 scant berry set and 2 plentiful berries. Berry set records were taken on plants which had at least 7 flowers present or showed evidence of having produced at least 7 buds during the season. Indehiscence classes ranged from 0–2, where 0 signifies complete indehiscence, 1 scant pollen shed and 2 complete dehiscence. Anther measurements were taken with a Bausch and Lomb ocular micrometer while cytological smears were prepared by staining freshly collected anther contents with a 0.45 % propio-carmine solution. One hundred cells from the anthers of each plant were observed under a light microscope (100×) and the frequencies of normal pollen, sporads and shrivelled microspores were recorded. Anthers were grouped into two color classes, green and non-green. Anthers of the non-green class were either yellow and orange while anthers in the green class ranged from green to yellow-green or orange-green. Anther color class designations represent the most characteristic state of the plant at the time the note was taken. It does not imply that all the anthers on a plant fell into that class. χ^2 analyses were performed on fertility characters of F_1 populations and BC_1 families to determine whether differences existed between progenies containing sensitive and resistant cytoplasms.

Results

Significant differences between reciprocal F_1 progenies occurred in a number of morphological characteristics, particularly those concerning terminal and adjacent leaflet dimensions (Tables 2 and 3). Leaflets used for leaflet area measurements were at a more mature stage than those leaflets used in scoring leaflet dimensions. There was no evidence of a consistent pattern of cytoplasmic control over these characteristics. The crossing direction showing higher values depended principally on the individual parental clones used. For example, significantly higher terminal leaflet areas were observed in progeny from $T_1 \times A_2$ and $T_2 \times A_3$ (both in ssp. *tuberosum* cytoplasm) and in $A_3 \times T_3$ and $PC \times T_2$ (both not in ssp. *tuberosum* cytoplasm) crosses when compared to their

Table 2. Morphological traits in F_1 reciprocal crosses of *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena*.

	$T_1 \times A_1$ and reciprocal[1]				$T_1 \times A_2$ and reciprocal				$T_2 \times A_3$ and reciprocal				$T_3 \times A_3$ and reciprocal			
	n*	[T]	[A]	P	n	[T]	[A]	P	n	[T]	[A]	P	n	[T]	[A]	P
F_1 populations, field 1978[2]																
Adjacent leaflet length[3] (cm)	36/65	3.1	3.4	0.02	50/65	4.0	4.6	0.001	56/59	3.7	3.5	0.11	55/55	3.5	3.7	0.19
Adjacent leaflet width[4] (cm)	36/65	3.8	3.9	0.85	50/65	2.7	2.8	0.93	56/59	4.4	4.2	0.29	55/55	4.1	3.6	0.003
Terminal leaflet length[5] (cm)	36/65	4.5	4.8	0.06	50/65	5.21	5.5	0.07	56/59	5.5	5.2	0.12	55/55	5.3	5.2	0.75
Leaf area terminal leaflet[6] (cm^2)	27/47	9.2	9.1	0.84	49/57	9.9	8.6	0.001	53/50	12.4	10.5	0.007	50/49	11.6	12.9	0.02
Leaf area adjacent leaflet[7] (cm^2)	27/47	5.4	6.3	0.02	49/57	6.7	5.9	0.02	53/50	8.4	7.4	0.02	50/49	7.9	8.9	0.004
Leaf angle[8] (°)	36/65	51.9	53.6	0.38	50/65	58.7	56.2	0.10	56/59	55.9	55.5	0.80	55/55	54.7	57.4	0.05
Interjected leaflets[9] (n)	23/35	3.8	4.1	0.70	29/32	5.9	5.2	0.25	23/16	8.4	6.8	0.01	41/41	6.0	5.5	0.35
Tuber weight[10] (g)	32/73	848.6	1000.1	0.05	49/51	921.6	925.6	0.96	51/49	948.8	870.8	0.42	50/64	1143.8	973.8	0.08
Tuber number[11]	32/73	16.1	17.3	0.57	49/51	16.5	15.1	0.51	51/49	13.0	11.3	0.36	50/64	26.0	21.0	0.12
Average tuber weight[12] (g)	32/73	52.7	57.8	0.55	49/51	55.9	61.3	0.70	51/49	73.0	77.1	0.51	50/64	44.0	46.4	0.91
Eye depth[13] (mm)	26/47	2.6	2.7	0.87	41/51	1.8	1.8	0.90	46/52	2.5	2.7	0.85	35/60	2.3	2.2	0.91
F_1 populations, greenhouse 1978[14]																
Tuber weight[10] (g)	31/48	17.7	22.2	***	46/46	17.9	20.6	ns	56/59	30.5	26.1	**	46/54	22.3	26.0	**
Tuber number[11]	31/48	1.4	1.7	**	46/46	1.8	1.9	ns	56/59	1.9	1.8	ns	46/54	1.6	1.8	ns
Average tuber weight[12] (g)	31/48	12.6	13.0	**	46/46	9.9	10.8	ns	56/59	16.1	14.5	**	46/54	13.9	14.4	ns

* Numerator = [T] individuals per mean; denominator = [P] per mean - *Nenner* = [T] *Individuen pro Mittelwert; Zähler* = [P] *pro Mittelwert* - *Numérateur* = [T] *individuels pour moyenne; dénominateur* = [P] *pour moyenne.*

* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001; n.s. = not significant - *nicht signifikant* - *non significatif*

[1] *Und reziprok* - *Et réciproques;* [2] *F_1-Populationen im Feld 1978* - *Populations de F_1 cultivées au champ en 1978;* [3] *Seitliche Blättchen, Länge* - *Folioles adjacentes, longueur;* [4] *Breite* - *Largeur;* [5] *Endfiederblättchen* - *Foliole terminale;* [6] *Blattfläche des Endfiederblättchens* - *Surface foliaire de la foliole terminale;* [7] *Blattfläche der Seitenblättchen* - *Surface foliaire de la foliole adjacente;* [8] *Blattstellungswinkel* - *Angle de la feuille;* [9] *Eingeschobene Blättchen* - *Folioles intercalaires;* [10] *Knollengewicht* - *Poids du tubercule;* [11] *Knollenzahl* - *Nombre de tubercules;* [12] *Durchschnittliches Knollengewicht* - *Poids moyen par tubercule;* [13] *Augentiefe* - *Enfoncement des yeux;* [14] *F_1-Populationen im Gewächshaus 1978* - *Populations de F_1 cultivées en serre en 1978*

Tabelle 2. Morphologische Merkmale in F_1 reziproken Kreuzungen von *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena*.
Tableau 2. Caractères morphologiques des F_1 réciproques obtenus par croisement de *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena*.

Table 3. Morphological traits in F_1 reciprocal crosses of *Solanum tuberosum* ssp. *tuberosum* × *(S. phureja* × *S. chacoense).*

	T_1 × PC and reciprocal[1]				T_4 × PC and reciprocal				T_2 × PC and reciprocal			
	n[+]	[T]	[P]	P	n	[T]	[P]	P	n	[T]	[P]	P
F_1 populations, field 1978[2]												
Adjacent leaflet length[3] (cm)	60/54	4.9	4.6	0.06	54/56	3.3	3.5	0.33	56/55	3.5	3.3	0.09
Adjacent leaflet width[4] (cm)	60/54	3.3	2.9	0.01	54/56	4.6	4.7	0.41	56/55	4.9	4.7	0.12
Terminal leaflet length[5] (cm)	60/54	5.3	5.2	0.44	54/56	5.1	5.5	0.06	56/55	5.9	5.8	0.44
Leaf area terminal leaflet[6] (cm^2)	51/50	12.6	12.3	0.60	52/52	12.6	12.5	0.89	51/51	14.5	17.3	0.0001
Leaf area adjacent leaflet[7] (cm^2)	51/50	9.8	8.5	0.005	52/52	10.8	10.7	0.73	51/51	11.2	13.2	0.0004
Leaf angle[8] (°)	51/49	50.5	48.9	0.87	54/54	56.9	49.8	0.09	53/52	47.4	55.2	0.12
Interjected leaflets[9] (n)	60/54	6.0	5.9	0.22	54/56	5.6	5.7	0.74	54/54	5.6	5.6	0.90
Tuber weight[10] (g)	50/50	1970.0	1021.4	0.0001	48/73	1954.5	1301.4	0.0001	24/70	2193.4	1371.7	0.0007
Tuber number[11]	50/50	36.9	22.4	0.0001	48/73	32.6	24.9	0.01	24/70	28.1	20.9	0.02
Average tuber weight[12] (g)	50/50	53.2	45.5	0.89	48/73	60.0	52.3	0.08	24/70	78.1	65.6	0.31
Eye depth[12] (mm)	49/46	2.9	2.5	0.81	40/74	2.8	2.5	0.80	50/69	2.9	2.7	0.82
F_1 populations, greenhouse 1978[14]												
Tuber weight[10] (g)	46/45	29.4	23.2	***	46/45	28.4	27.6	ns	45/45	28.3	28.8	ns
Tuber number[11]	46/45	2.2	2.0	**	46/45	2.1	2.1	ns	45/45	1.8	2.0	ns
Average tuber weight[12] (g)	46/45	13.4	11.6	**	46/45	13.5	13.1	ns	45/45	15.7	14.4	ns

[+], *, **, ***, n.s. See Table 2 - *Siehe Tabelle 2 - Voir tableau 2.*

[1-14] *Siehe Tabelle 2 - Voir tableau 2*

Tabelle 3. Morphologische Merkmale in F_1 reziproken Kreuzungen von *Solanum tuberosum* ssp. *tuberosum* × *(S. phureja* × *S. chacoense).*
Tableau 3. Caractères morphologiques des F_1 réciproques obtenus par croisement de *Solanum tuberosum* ssp. *tuberosum* × *(S. phureja* × *S. chacoense).*

reciprocals. However, while differences between reciprocals occurred in some F_1 combinations, the overall lack of significant differences was more striking than was their presence.

The tuber characteristics of reciprocal F_1 populations were evaluated under field (1978) and greenhouse conditions. Plants were grown from true seed (field 1978) and replanted as tuber seed (greenhouse). The only significant differences in tuber characteristics observed in field trials occurred between reciprocal progeny of the T × PC crosses. In each case values for tuber number and weight were on average higher in progenies containing ssp. *tuberosum* cytoplasm. In greenhouse trials, the pattern of reversing reciprocal differences observed with leaflets area characteristics was evident in T × A crosses for tuber characteristics. The only cross which showed consistent reciprocal differences for tuber characteristics in both field and greenhouse environments was $T_1 \times PC_1$ in which progenies containing ssp. *tuberosum* cytoplasm were superior to their reciprocal counterparts.

BC_1 families involving $T_1 \times (A_2 \times T_1)$, $T_5 \times (PC \times T_6)$ and $T_1 \times (PC \times T_1)$ crosses showed significant differences between reciprocals (Table 4). While significant differences occurred between reciprocals of these crosses, there were comparatively fewer than those in the F_1. BC_1 contrasts were sporadic and did not follow those seen in the F_1.

The phenotypic characters used to measure rates of progression were those used by Simmonds (1964) and Hawkes (1956). These included: (1) adjacent leaflet width and length and terminal leaflet length; (2) leaf area of adjacent and terminal leaflets; (3) leaf angle; and (4) number of interjected leaflets. An analysis of variance test for normality (Shapiro & Wilk, 1965) was performed on all phenotypic characters. All characters except leaf angle and interjected leaflets had normal distributions in both F_1 and BC_1. These two characters had continuous distributions in both F_1 and BC_1 though they did differ significantly from a strictly normal distribution. These data indicate that all characters were under polygenic control.

The F_1 represents the initial insertion of chromosomal genes of ssp. *tuberosum* into the cytoplasmic background of *andigena* or *phureja* and the interaction effects of these distinctly different genomes. This interaction and the rate of progression of phenotypic characteristics towards a recurrent ssp. *tuberosum* parent (T_1) was evaluated utilizing A_1, A_2, and PC as non-recurrent parents. The mean values of phenotypic characters in F_1 and BC_1 progeny bracketed by their 95 % confidence limits for populations involving T_1 are given in Fig. 1–3. Findings of this evaluation were compared to data when all sets of progeny families were taken collectively (Table 5).

The F_1 progenies from reciprocal T × A crosses are closer to the *andigena* parent in terminal and adjacent leaflet dimensions than to the *tuberosum* parent (Fig. 1, 2, and 3). These facts reflect the dominance of *andigena* parental genes governing these parameters. In contrast to the leaf dimension characteristics, the low number of interjected leaflets and larger leaf angles, typical of ssp. *tuberosum*, are dominant to the higher number of interjected leaflets and smaller angles of ssp. *andigena*. This resulted in transgressive segregation in the F_1 for these characters. When sets of F_1 progeny families in T × A reciprocal crosses are taken collectively (Table 5), observations of all characters parallel results obtained in $T_1 \times A_1$ and $T_1 \times A_2$ reciprocal matings, except adjacent leaflet width. Progenies showed the dominance of ssp. *tuberosum* parental genes for this character. Although leaf angle means were too close to allow discrimination between

Table 4. Morphological traits in reciprocal backcross sib families from crosses of (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) and ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]). First backcross families.

Morphological characteristic[14]	$T_i \times (A_1 \times T_1)$ and reciprocal[1]				$T_i \times (A_2 \times T_1)$ and reciprocal			
	n[1]	[T]	[A]		n	[T]	[A]	
Adjacent leaflet length[3] (cm)	341/298	5.0	5.0	ns	214/119	4.9	5.7	**
Adjacent leaflet width[4] (cm)	341/298	3.1	3.1	ns	214/119	3.0	3.2	ns
Terminal leaflet length[5] (cm)	341/298	6.9	7.02	ns	214/119	6.6	5.9	*
Leaf area terminal leaflet[6] (cm^2)	332/288	17.3	16.5	ns	212/98	15.6	16.1	ns
Leaf area adjacent leaflet[7] (cm^2)	332/288	10.0	10.0	ns	212/98	9.4	10.4	ns
Leaf angle[8]	340/297	48.6	49.5	ns	214/119	51.2	48.7	ns
Interjected leaflets[9] (n)	340/297	3.8	3.8	ns	225/94	4.6	6.2	**
Petiolule[15] (mm)	341/298	3.1	2.9	ns	214/119	3.9	5.5	**
Style thickness[16] (mm)	365/316	0.4	0.3	ns	90/51	0.3	0.4	ns
Tuber weight[10] (g)	346/297	1046.9	1042.3	ns	220/97	1120.0	1259.3	ns
Tuber number[11]	344/297	22.8	24.3	ns	220/97	26.5	30.9	*
Average tuber weight[12] (g)	344/297	45.9	42.8	ns	220/97	42.2	40.7	ns
Eye depth[13] (mm)	213/185	2.3	2.3	ns	100/111	1.8	1.9	ns
Sets of reciprocals[17]	4				2			

+, *, **, ***, n.s. See Table 2 - *Siehe Tabelle 2 - Voir tableau 2.*

[1, 13] *Siehe Tabelle 2 - Voir tableau 2;* [14] *Morphologische Merkmale - Caractéristiques morphologiques;* [15] *Blütenblättchen Pétiolule;* [16] *Dicke des Stempels - Epaisseur du style;* [17] *Zahl der Reziproken - Classes de réciprocité*

Tabelle 4. Morphologische Merkmale in reziproken Rückkreuzungsfamilien aus Kreuzungen von (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) und ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]). Familien der ersten Rückkreuzung.

Tableau 4. Caractères morphologiques des familles réciproques issues du croisement en retour de (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) et ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]). Premières familles issues du croisement en retour.

parents, transgressive values were recorded.

While F_1 progeny of reciprocal $T_1 \times$ PC matings reflected dominance of the *tuberosum* parental genes for leaf angle, the characters interjected leaflets, and adjacent and terminal leaflet lengths were more influenced by those of the PC parent. These trends parallel those when sets of progeny families were taken collectively (Table 5), except for adjacent leaflet length and width. Adjacent leaflet width showed the dominance of *tuberosum* genes and length was more influenced by the PC parent. In all cases, leaflet areas obtained mid-point values as in reciprocal $T_1 \times$ PC matings.

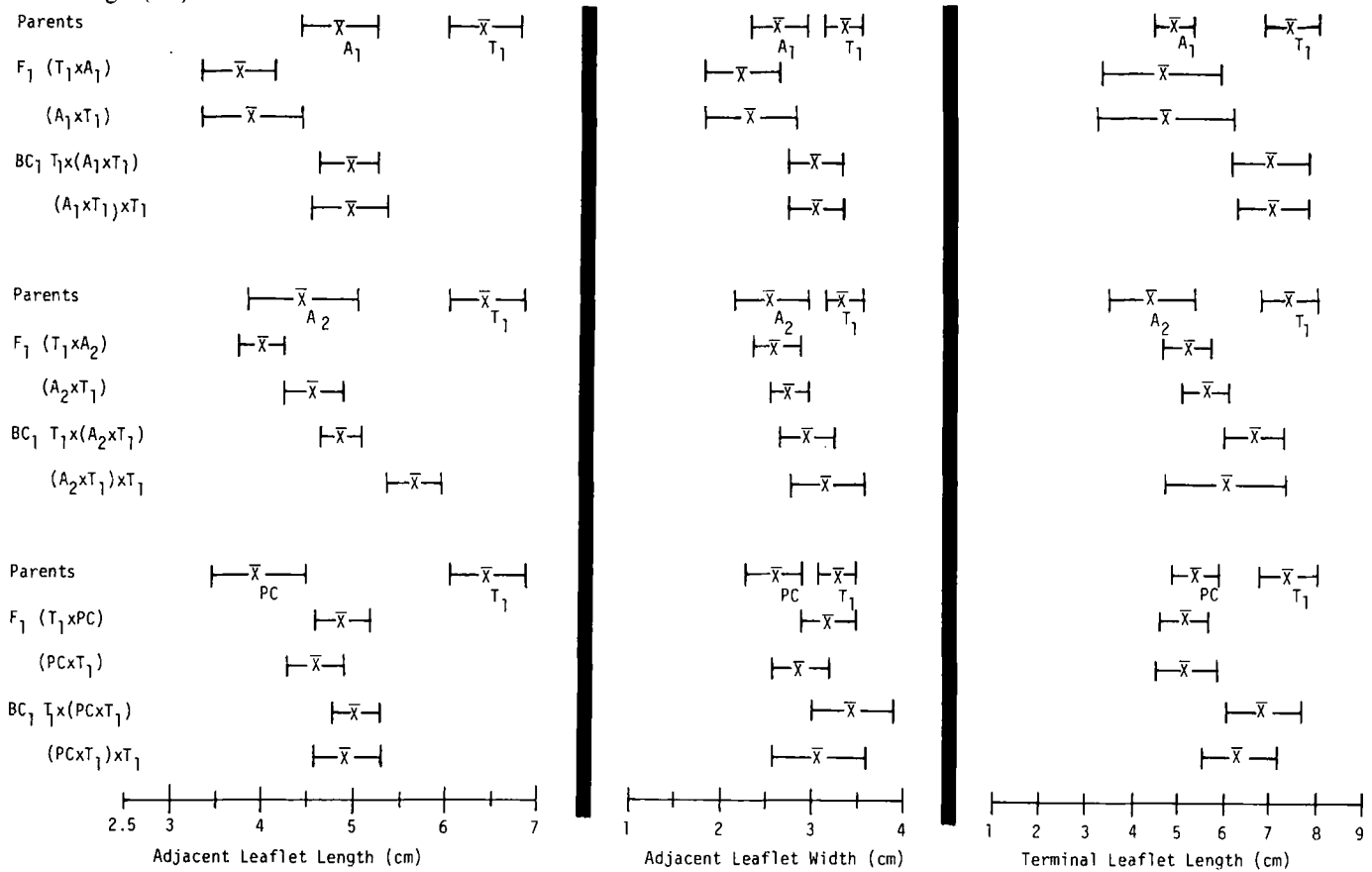
Progress towards the ssp. *tuberosum* parental morphology occurred for all character-

$T_5 \times (PC \times T_5)$ and reciprocal				$T_5 \times (PC \times T_6)$ and reciprocal				$T_1 \times (PC \times T_1)$ and reciprocal			
n	[T]	[P]		n	[T]	[P]		n	[T]	[P]	
301/204	4.8	4.5	ns	100/20	4.6	4.5	ns	98/158	5.0	4.9	ns
301/204	3.2	3.0	ns	100/20	3.0	2.7	ns	98/158	3.5	3.1	*
301/204	6.6	6.6	ns	100/20	6.2	6.5	ns	98/158	6.7	6.3	*
292/119	18.0	17.1	ns	96/22	15.0	14.6	ns	119/153	16.2	15.7	ns
292/119	10.1	9.0	ns	96/22	8.6	8.0	ns	119/153	9.7	9.0	ns
298/206	44.0	42.3	ns	99/21	44.0	44.1	ns	95/158	48.2	47.3	ns
301/204	4.4	5.0	ns	100/20	4.9	4.1	ns	98/158	5.2	5.3	ns
301/204	4.6	4.6	ns	100/20	6.1	5.1	**	98/158	5.1	5.1	ns
320/217	0.4	0.4	ns	114/24	0.5	0.4	ns	94/119	0.5	0.5	ns
279/197	948.9	822.0	ns	105/22	1057.7	723.6	*	116/152	1000.3	946.8	ns
279/197	16.1	15.1	ns	105/22	17.8	18.9	ns	116/152	22.4	23.1	ns
279/197	58.8	54.5	ns	105/22	59.3	38.1	*	116/152	44.6	41.0	ns
193/168 4	2.4	2.4	ns	54/21 1	1.9	2.0	ns	70/69 2	2.6	2.9	ns

istics in BC_1, i.e. $(A \times T_1) \times T_1$, $(PC \times T_1) \times T_1$ and reciprocals (Fig. 1-3). In $A \times T$ matings mean values for the character adjacent leaflet length were essentially those of the *andigena* parent while terminal leaflet length and terminal and adjacent leaflet areas were closer to the *tuberosum* parent. Mean values for adjacent leaflet width had obtained parental mid-point values by the BC_1. Leaf angle and interjected leaflets had obtained *tuberosum*-like values by the F_1, due to tuberosum dominance for these characters. When sets of progeny families are considered collectively (Table 5) progress toward the recurrent parent was observed but was not as striking as that seen in $A\text{-}T_1$ matings.

For $PC\text{-}T_1$ matings mean values for adjacent leaflet length and interjected leaflets were

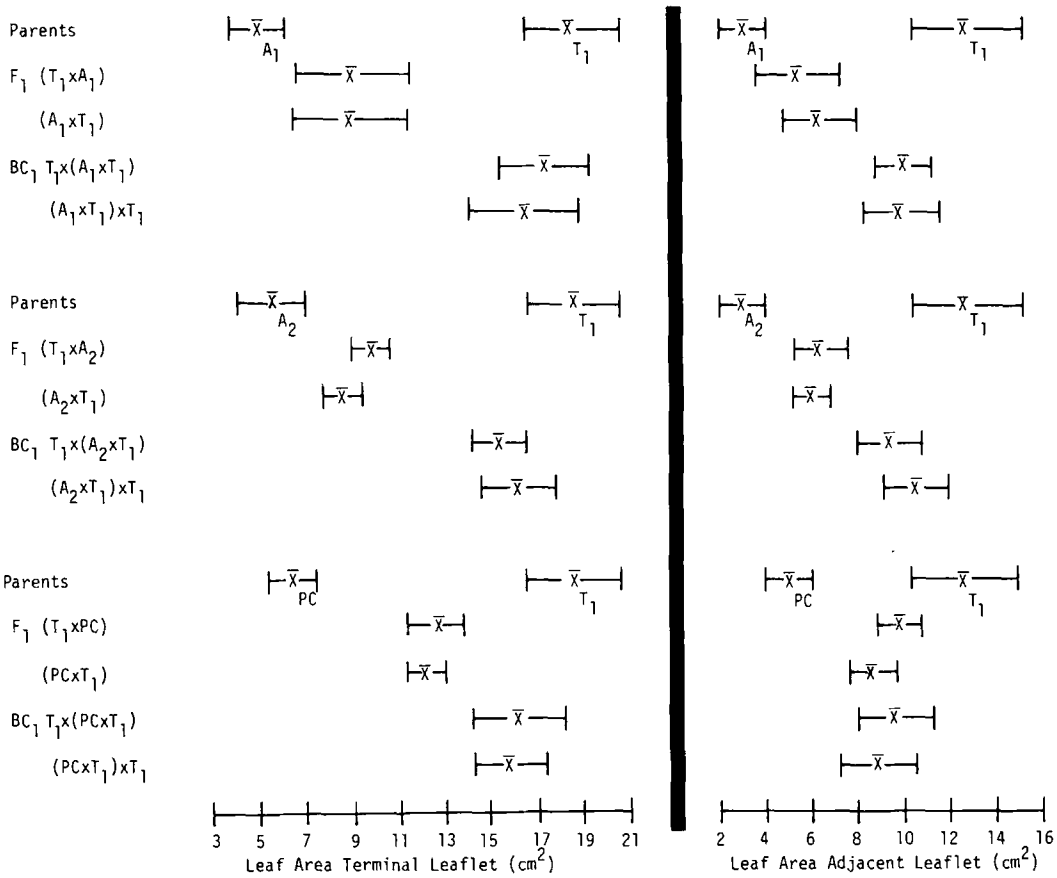
Fig. 1. Morphological characters of parental clones and reciprocal F_1 and BC_1 progeny. Means of adjacent leaflet length, width, and terminal leaflet length (cm).



Adjacent leaflet length (cm) - *Länge der Seitenblättchen - Longueur de la foliole adjacente*
Adjacent leaflet width (cm) - *Breite der Seitenblättchen - Largeur de la foliole adjacente*
Terminal leaflet length (cm) - *Länge der Endfiederblättchen Longueur de la foliole terminale*
Parents - *Eltern - Parents*

Abb. 1. Morphologische Merkmale der Elternklone und der reziproken F_1 und BC_1-Nachkommenschaften. Mittelwerte der Länge und Breite der Seitenblättchen und der Länge der Endfiederblättchen (cm).
Fig. 1. Caractères morphologiques des clônes parentaux et de la descendance réciproque des F_1 et BC_1. Moyenne des longueurs et largeurs de la foliole adjacente et de la longueur de la foliole terminale (cm).

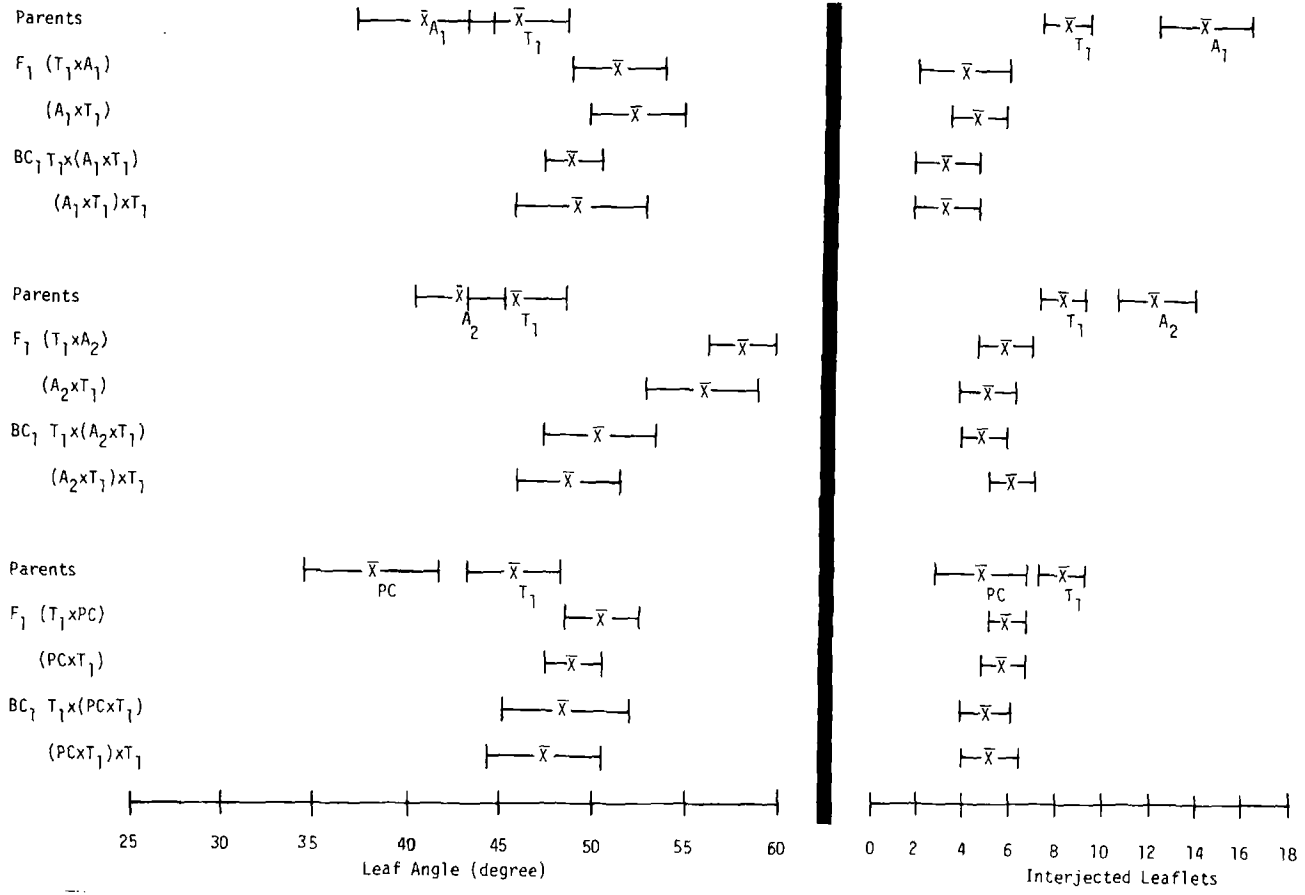
Fig. 2. Morphological characters of parental clones and reciprocal F_1 and BC_1 progeny. Means of area terminal and adjacent leaflet (cm^2).



Leaf area terminal leaflet (cm^2) - *Blattfläche des Endfiederblättchen - Surface foliaire de la foliole terminale*
Leaf area adjacent leaflet (cm^2) - *Blattfläche der Seitenblättchen - Surface foliaire de la foliole adjacente*
Parents - *Eltern - Parents*

Abb. 2. Morphologische Merkmale der Elternklone und der reziproken F_1 und BC_1-Nachkommenschaften. Mittelwerte der Blattfläche der Endfieder- und Seitenblättchen (cm^2).
Fig. 2. Caractères morphologiques des clônes parentaux et de la descendance réciproque des F_1 et BC_1. Moyennes des surfaces des folioles terminales et adjacentes (cm^2).

Fig. 3. Morphological characters of parental clones and reciprocal F_1 and BC_1 progeny. Means of leaf angle and interjected leaflets.



Leaf angle (degrees) - *Blattstellungswinkel (Grade) - Angle de la feuille (degré)*
Interjected leaflets - *Eingeschobene Blättchen Folioles intercalaires*
Parents - *Eltern - Parents*

Abb. 3. Morphologische Merkmale der Elternklone und der reziproken F_1 und BC_1-Nachkommenschaften. Mittelwerte der Blattstellungswinkel und der eingeschobenen Blättchen.
Fig. 3. Caractères morphologiques des clônes parentaux et de la descendance réciproque des F_1 et BC_1. Moyennes de l'angle de la feuille et des folioles intercalaires.

closer to the PC parent. Adjacent leaflet width, leaf angle, adjacent and terminal leaflet length and area were closer to mean values of the *tuberosum* parent. Progress towards ssp. *tuberosum* was comparatively slower when sets of progeny families are considered collectively.

In some instances the range of variation in morphological characters of parental clones was larger than the variation observed in segregating populations. The parents grown in replicated design were planted as tuber-seed while the reciprocal F_1's and BC_1's originated as seedlings. The parental range probably reflects the environmental differences between different replicates (the soil conditions in the field being rather non-uniform). The F_1 and BC_1 range reflects both the genetic influences and soil variations. However, since they were planted in a more uniform field they may not have been as subject to soil variations. The large numbers of F_1 and BC_1 progeny examined may also have been a factor in decreasing the variance.

Fertility data were taken on F_1 and BC_1 progeny to determine whether the sterility-resistant cytoplasmic factors of *andigena* and *phureja* retained their influence in advanced generations. Due to meager flowering of reciprocal F_1 ssp. *tuberosum* $\times$ ssp. *andigena* progeny, fertility notes were not taken on $T_3 \times A_3$ reciprocal F_1 lots and limited information was obtained on other T $\times$ A F_1 populations. However, significant differences were observed between reciprocal lots involving $T_1 \times A_1$, $T_1 \times A_2$ and $T_2 \times A_3$ crosses for berry set, anther length, and anther width, respectively (Table 6).

Those progeny containing the *S. phureja* cytoplasmic background [P] consistently showed higher female fertility than their reciprocals. For instance, progeny containing sterility-resistant cytoplasmic factors, i.e. PC $\times$ T crossings, displayed significantly greater numbers of non-green anthers and higher frequencies of normal pollen when compared to their reciprocal counterparts with sterility sensitive cytoplasmic backgrounds.

Fertility trends in BC_1 sib families (Table 7) parallel those observed in F_1 populations. All BC_1 families with an *andigena* or *phureja* cytoplasmic background had substantial fertility. With only a few exceptions - $T_1 \times (A_2 \times T_1)$ and $T_1 \times (PC \times T_1)$ - they were significantly different from their reciprocal counterparts in ssp. *tuberosum* cytoplasm for berry set, anther width and length, anther color, dehiscence ability and pollen fertility.

Discussion

The substitution backcross program described here was designed to overcome some of the cytoplasmic sterility problems associated with the ssp. *tuberosum* potato. This would consequently allow intraspecific and interspecific crosses to be made with formerly incompatible potato clones. By monitoring the progress towards a recurrent ssp. *tuberosum* parent during backcrossing, information was obtained which showed how rapidly ssp. *tuberosum*-plants can be regained in the changed cytoplasmic background.

Cytoplasm source did consistently influence morphological parameters relating directly to fertility (berry set, anther length and width, anther color and dehiscence, and pollen fertility) but not for other above and below ground parameters. Significant reciprocal differences in morphological characters did occur both in F_1 and BC_1 progeny, but the occurrence depended largely on the parents used.

When F_1 greenhouse and field populations in this study were examined for tuber

Table 5. Morphological traits of F_1 and BC_1 families and representative clones of *Solanum*.

Morphological characteristic[11]	*Solanum* clones[10]									F_1 populations[+1]					
										T × A and reciprocal[2]					
	*andigena**			*tuberosum***			PC***			[A]			[T]		
	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	X	(±) 95 %
Adjacent leaflet length[3] (cm)	45	4.2	0.46	450	6.1	0.35	20	3.9	0.70	244	3.8	0.06	197	3.6	0.14
Adjacent leaflet width[4] (cm)	45	2.4	0.27	450	3.8	0.18	20	2.6	0.30	244	3.6	0.12	197	3.8	0.10
Terminal leaflet length[5] (cm)	45	5.9	0.63	450	9.1	0.62	20	5.3	0.30	244	5.2	0.14	197	5.1	0.16
Leaf area terminal leaflet[6] (cm^2)	45	6.3	1.6	450	23.0	0.96	20	6.8	0.40	203	10.3	0.72	179	10.8	0.44
Leaf area adjacent leaflet[7] (cm^2)	45	4.0	1.4	450	16.3	0.88	20	5.3	0.70	203	7.1	0.60	179	7.1	0.42
Leaf angle[8]	45	42.2	2.2	450	45.6	3.8	20	38.1	4.0	244	55.7	0.98	197	55.3	1.22
Interjected leaflets[9]	45	12.1	2.8	450	9.0	2.2	20	4.2	2.4	124	5.4	0.50	116	6.0	0.56
Sets of progeny families[12]										4			4		

	BC_1 populations																	
	T × P and reciprocal						T × (A × T) and reciprocal						T × (PC × T) and reciprocal					
	[T]			[P]			[A]			[T]			[T]			[P]		
	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %	N	$\bar{X}$	(±) 95 %
Adjacent leaflet length[3] (cm)	170	3.9	0.10	165	3.8	0.10	417	5.4	0.08	555	5.0	0.06	499	4.8	0.08	382	4.6	0.10
Adjacent leaflet width[4] (cm)	170	4.3	0.14	165	4.1	0.14	417	3.2	0.12	555	3.1	0.08	499	3.2	0.10	382	2.9	0.14
Terminal leaflet length[5] (cm)	170	5.4	0.18	165	5.5	0.18	417	6.6	0.26	555	6.7	0.16	499	6.5	0.18	382	6.5	0.30
Leaf area terminal leaflet[6] (cm^2)	154	13.3	0.50	153	14.0	0.60	386	16.3	0.56	544	16.4	0.38	507	16.4	0.32	294	15.8	0.72
Leaf area adjacent leaflet[7] (cm^2)	154	10.6	0.40	153	10.8	0.54	386	10.2	0.42	544	9.7	0.30	507	9.5	0.40	294	8.6	0.52
Leaf angle[8]	158	51.6	0.40	155	51.3	0.40	416	49.1	1.12	554	49.9	0.68	492	45.4	0.80	385	44.6	1.22
Interjected leaflets[9]	164	5.7	1.12	164	5.7	1.28	391	5.0	0.34	562	4.2	0.22	499	4.8	0.32	382	4.8	0.44
Sets of progeny families[12]	3			3			6			6			7			7		

* Based on 15 ssp. *andigena* clones arranged in 3 replications with one observation. Clones include those in Table 1 plus R122-18, 122-5, 221-3, 142-6, 112-1, 143-10, 123-34, 293-12, 221-9, 656-3, S 521-7, 505-11 from Dr R. Plaisted - *Basierend auf 15 ssp. andigena-Klonen, zusammengestellt in 3 Wiederholungen mit einer Beurteilung. Die Klone umfassen die in Tabelle 1 genannten und zusätzlich R122-18 . . . Sur la base de 15 clônes ssp. andigena répartis sur 3 répétitions avec une observation. Clônes du tableau 1 inclus, plus R122-18 . . .*

** Based on 10 ssp. *tuberosum* clones arranged in 3 replications and 15 observations per replication. Clones include those in Table 1 plus cvs. Atlantic, Green Mountain, Monona, and Penn 71 *Basierend auf 10 ssp. tuberosum-Klone, zusammengestellt in 3 Wiederholungen und 15 Beurteilungen pro Wiederholung. Die Klone umfassen die in Tabelle 1 genannten und zusätzlich Atlantic, Green Mountain, Monona und Penn 71 - Sur la base de 10 clônes tuberosum répartis sur 3 répétitions avec 15 observations. Clônes du tableau 1 inclus, plus Atlantic, Green Mountain, Monona et Penn 71.*

*** Collected from cloned single hill spaced plantings of a *(S. phureja × S. chacoense)* hybrid - *Gesammelt von geklonten Einzelpflanzen einer (S. phureja × S. chacoense) Hybride Récolté à partir d'un rang unique d'hybrides de (S. phureja × S. chacoense).*

† Individual single hill spaced seedlings of progeny families each scored once *Individuelle Einzelpflanzen von Nachkommenschaftsfamilien, jede einzeln beurteilt A partir d'une seule semence pour chaque descendant des familles.*

[1] *Populationen - Populations;* [2-9] *Siehe Tabelle 2 Voir tableau 2;* [10] *Klone von Solanum Clônes de Solanum;* [11] *Morphologische Merkmale - Caractéristiques morphologiques;* [12] *Zahl der Nachkommenschaftsfamilien Classes des familles de la descendance*

Tabelle 5. Morphologische Merkmale von F_1- und BC_1-Familien und repräsentativen Klonen von *Solanum*.
Tableau 5. Caractères morphologiques des familles F_1 en BC_1 et clônes représentatifs de *Solanum*.

Table 6. Anther and berry characters of F_1 reciprocal crosses of *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena* and ssp. *tuberosum* × *(S. phureja* × *S. chacoense).* Fertility of reciprocal F_1 populations 1978.

	Berry set, classes[+1]				Anther[2]			Anther color[5]			Anther contents[8]			
	total	0	1	2	n	width[3] (mm)	length[4] (mm)	n	green[6]	non-green[7]	n	sporads	shrivelled microspores[9]	normal pollen[10]
$T_1 \times A_1$	26	26	0	0	10	2.75	6.90							
Reciprocal[11]	43	25	18	0	11	2.64	6.95							
		**				ns	ns							
$T_1 \times A_2$	76	69	6	1	10	2.40	6.46							
Reciprocal	95	85	6	4	10	2.64	7.30							
		ns				ns	**							
$T_2 \times A_3$	117	117	0	0	8	2.35	7.78							
Reciprocal	35	32	3	0	13	2.75	7.67							
		ns				**	ns							
$T_1 \times PC$	51	29	10	12	55	1.95	6.04	60	32	28	37	22	9	6
Reciprocal	56	0	0	56	50	2.29	6.95	50	0	50	36	0	4	32
		***				***	***		***			***		
$T_4 \times PC$	51	11	29	11	42	1.7	5.90	42	34	8	36	4	15	17
Reciprocal	55	2	9	44	47	2.4	6.80	49	0	49	36	0	7	29
		***				***	***		***			***		
$T_2 \times PC$	49	34	13	2	45	2.0	6.20	45	30	15	36	23	4	9
Reciprocal	54	0	6	48	50	2.4	7.30	49	0	49	36	0	5	31
		***				***	***		***			***		

[+] 0 = no berry set - *Kein Beerenansatz - Pas de fruits;* 1 = scant berry set - *Geringer Beerenansatz - Peu de fruits;* 2 = plentiful berry set - *Reichlicher Beerenansatz - Beaucoup de fruits.*
*, **, ***, ns See Table 2 - *Siehe Tabelle 2 - Voir tableau 2*

[1] *Beerenansatz, Klassen - Classes en fonction de la fructification;* [2] *Anthere - Anthère;* [3] *Breite - Largeur;* [4] *Länge - Longueur;* [5] *Antherenfarbe - Couleur de l'anthère;* [6] *Grün - Vert;* [7] *Nicht grün - Non vert;* [8] *Antherenінhalt - Contenu de l'anthère;* [9] *Verkümmerte Mikrosporen - Microspores ratatinées;* [10] *Normale Pollen - Pollen normal;* [11] *Reziprok - Réciproque*

Tabelle 6. Merkmale der Antheren und Beeren von F_1-Reziprokkreuzungen von *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena* und ssp. *tuberosum* × *(S. phureja* × *S. chacoense).* Fruchtbarkeit der reziproken F_1-populationen 1978.
Tableau 6. Caractères de l'anthère et du fruit de F_1 réciproques issus du croisement de *Solanum tuberosum* ssp. *tuberosum* × ssp. *andigena* et ssp. *tuberosum* × *(S. phureja* × *S. chacoense).* Fertilité des populations de F_1 réciproques en 1978.

Table 7. Anther and berry characters of reciprocal backcross sib families from crosses of (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) and ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]). Fertility of reciprocal BC_1 families 1979.

	Berry set, classes[+,1]				Anther[2]			Anther color[5]			Indehiscence classes[++,12]				Anther content[8]			
	total	0	1	2	n	width[3] (mm)	length[4] (mm)	n	green[6]	non-green[7]	total	0	1	2	n	sporads	shrivelled microspores[9]	normal pollen[10]
$T_1 \times (A_1 \times T_1)$	157	104	7	46	159	2.31	6.18	159	54	105	82	23	19	40	355	33	72	250
Reciprocal[11]	143	73	14	56	133	2.78	6.65	134	20	114	52	3	0	49	301	0	11	290
		**				**	**		***			***				***		
$T_1 \times (A_2 \times T_1)$	94	61	4	9	90	2.33	6.19	91	37	54	29	2	10	17	214	12	47	155
Reciprocal	52	31	4	17	51	2.72	6.67	50	13	37	16	0	0	16	98	0	0	98
		ns				**	**		ns			**				***		
$T_5 \times (PC \times T_5)$	156	131	6	19	154	2.23	5.81	154	108	30	75	42	19	14	456	105	285	66
Reciprocal	115	62	8	45	114	2.57	6.52	113	46	83	57	2	6	49	204	0	13	191
		***				**	***		***			***				***		
$T_5 \times (PC \times T_6)$	71	49	4	18	69	2.06	5.73	69	46	23	39	24	8	7	101	24	15	61
Reciprocal	15	3	0	12	16	2.48	6.39	16	3	13	7	0	0	7	21	0	4	17
		***				**	**		***			***				***		
$T_1 \times (PC \times T_1)$	103	41	9	53	94	2.27	6.27	95	47	48	55	7	12	36	121	9	14	98
Reciprocal	119	27	7	85	119	2.54	6.51	119	42	77	65	7	6	52	149	0	4	145
		**				**	**		*			ns				***		

[+] See Table 6 – *Siehe Tabelle 6* – *Voir tableau 6.*
[++] 0 = indehiscence, 1 = partial dehiscence, 2 = dehiscence – *0 = kein Aufspringen, 1 = teilweise Aufspringen, 2 = Aufspringen* – *0 = indéhiscence, 1 = déhiscence partielle, 2 = déhiscence.*
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s. = not significant – *nicht significant* – *non significatif.*

[1, 11] *Siehe Tabelle 6* – *Voir tableau 6;* [12] *Aufspringen, Klassen* – *Classes d'indéhiscence.*

Tabelle 7. Antheren- und Beerenmerkmale von Reziproken-Rückkreuzungsfamilien aus Kreuzungen von (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) und ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]).

Tableau 7. Caractères de l'anthère et du fruit des familles réciproques issues de croisement en retour de (*S. tuberosum* ssp. *andigena* × ssp. *tuberosum*[2]) et ((*S. phureja* × *S. chacoense*) × ssp. *tuberosum*[2]).

weight, number and average tuber weight, only one consistent reciprocal difference ($T_1 \times PC$) was observed in which higher values were produced by progenies with a [T] background. In all other crosses, differences that were recorded in the field (botanical seed) were not seen in the greenhouse (seed tuber) and vice-versa. Moreover these differences were not observed in the reciprocal BC_1 progeny, $T_1 \times (PC \times T_1)$.

These data support findings of Rothacker (1962) in which tuber yield/hill, tuber number and size were influenced by the specific ssp. *tuberosum* parent used in ssp. *andigena*-ssp. *tuberosum* crosses. It seems likely that such reciprocal differences resulted from maternal effects, i.e. an influence of the chromosomal gene products of the maternal parent on the progeny. Had they been true cytoplasmic effects they would have been more consistently maintained in the backcross progeny. This conclusion is of practical importance. If tuber yield is partially cytoplasmically determined then some productive potential may be lost as a result of cytoplasmic substitution. If it is subject only to maternal effects, the production loss would disappear during backcrossing.

Hybrids involving ssp. *andigena* and ssp. *tuberosum* have been made and yield components examined. In terms of total yield $T \times A$ or $A \times T$ hybrids were superior to either parental subspecies alone (Cubillos & Plaisted, 1976; Glendinning, 1969; Paxman, 1966; Tarn & Tai, 1977). $T \times A$ sometimes (Cubiloos & Plaisted, 1976; Hoopes et al., 1980; Tarn & Tai, 1977), but not always (Tarn & Tai, 1973, 1977) exceeds $A \times T$ in numbers of tubers. Hoopes et al. (1980) and Sanford & Hanneman (1979) both showed differences in tuber yield between reciprocal F_1 progenies. Long-time (seven years) maintenance of the reciprocal differences (Hoopes et al., 1980) led the authors to favor a cytoplasmic interpretation since dilution of original maternal products might be expected to occur with time. The Sanford & Hanneman (1979) yield differences also seemed more amenable to a cytoplasmic interpretation since they were maintained into the F_2 generation. However, a definitive answer would require reciprocal backcross progenies.

Backcrossing studies on A and T matings (Rothacker, 1962) have shown that standard values (cv. Ackersegen) for tuber yield, tuber number, tuber size and starch content were reached by the BC_1 and no substantial improvements were seen in the BC_2. Data from the present study indicate that although progenies may return towards characteristics occurring in the recurrent ssp. *tuberosum* parent by the BC_1, the rate of return depends upon the recurrent parent and the trait considered. Morphological characters of F_1 populations were influenced by dominant parental genes. For example, rate of progression towards the T_1 (Norchip) recurrent parent, in $T_1 \times A_1$ and $T_1 \times A_2$ reciprocal crosses, was rapid for numbers of interjected leaflets and leaf angle reaching *tuberosum*-like values by the F_1. While leaflet characters had reached mid-point values by the BC_1, only interjected leaflets and leaf angle obtained *tuberosum*-like characteristics. These types of trends were also evident in progenies of reciprocal $T_1 \times PC$ crosses.

Cytological evaluation of anther contents also provides an indication of the rate of return towards the recurrent *tuberosum* parent. When the male fertility of progeny in *tuberosum* cytoplasm in the F_1 ($T \times PC$) is compared to that of the BC_1 [$T \times (PC \times T)$] progeny, contrasts occur which demonstrate the replacement of *S. phureja* genes by ssp. *tuberosum* nuclear genes. For example, in the F_1 77 % (33 % sporads and 44 % with shrivelled microspores) of the progeny showed sterility resulting from the presence of *S. phureja* genes compared to 33 % (13 % sporads and 20 % with shrivelled microspores) in

the BC_1. This increase in fertility from the F_1 to BC_1 is close to the expected recovery rate of one half per generation.

It has not been demonstrated that progeny containing the sterility-resistant cytoplasmic factors of *andigena* or *phureja* have a higher degree of fertility when compared to reciprocal progeny in sterility-resistant *tuberosum* cytoplasm. This characteristic fertility was retained in the BC_1. This fact, in conjunction with seemingly non-cytoplasmic nature of the morphological traits studied, including tuber weight and number, indicates that the substitution backcrossing program may produce potentially useful breeding stock.

Zusammenfassung

Zytoplasmatische Evaluierungen während der Substitutions-Rückkreuzung in Solanum

Es wurde ein Substitutions-Rückkreuzungsprogramm entwickelt, um die zytoplasmatischen Faktoren von *Solanum tuberosum* L. ssp. *tuberosum* so zu ändern, dass eine Form entsteht, die keine Empfindlichkeit gegen dominante Gene für zytoplasmatische Sterilität aufweist. Sterilitäts-resistente zytoplasmatische Faktoren von *Solanum tuberosum* ssp. *andigena* (Juz. & Buk.) Hawkes und von *S. phureja* (Juz. & Buk.) wurden mit chromosomalen Genen von *S. tuberosum* spp. *tuberosum* kombiniert (Tabelle 1). Elf morphologische Merkmale der reziproken F_1 und BC_1 Nachkommenschaften wurden ausgewählt, um die Steigerungsrate gegenüber Merkmalen, die in den wiederholt vorkommenden ssp. *tuberosum* Eltern auftreten, zu beurteilen und um das Ausmass zu bestimmen, in dem das Zytoplasma die Form der Pflanze beeinflusst. Weibliche und männliche Fertilität der F_1 und BC_1 Populationen wurden auch evaluiert. Die morphologischen Merkmale wurden durch die zytoplasmatischen Faktoren nicht einheitlich beeinflusst, mit Ausnahme der direkt mit der Fruchtbarkeit verbundenen Parameter (Tabellen 6 und 7). Die Unterschiede zwischen reziproken Nachkommenschaften hingen mehr von den Genen der bei der Kreuzung verwendeten individuellen Eltern ab, als von der zytoplasmatischen Herkunft (Tabellen 2–5). In den Knollenmerkmalen traten keine beständigen reziproken Unterschiede auf und die Unterschiede, die auftraten, schienen eher einen mütterlichen als einen zytoplasmatischen Einfluss aufzuweisen (Tabellen 2–5). F_1 und BC_1 Nachkommenschaften, die die Sterilitätsresistenten zytoplasmatischer Faktoren von ssp. *andigena* oder *S. phureja* enthielten, hatten eine höhere Fertilität als ihre reziproken Nachkommenschaften mit Zytoplasma von ssp. *tuberosum* (Tabellen 6 und 7). Die Verteilung der F_1 und BC_1 Werte für alle morphologischen Merkmale, die zur Kennzeichnung der Eltern verwendet worden waren, zeigte ihren polygenen Charakter. Eine Dominanz der *tuberosum*-Gene zeigte sich in der Blattstellung und bei den eingeschobenen Blättchen (Abb. 3), während die Merkmale der Blättchen eine Dominanz der *andigena*-Gene anzeigte (Abb. 1 und 2). Die Steigerungsrate in Richtung ssp. *tuberosum* war bei dem Blattstellungswinkel und der Zahl der eingeschobenen Blättchen (Abb. 3) schnell, denn in der F_1-Generation wurden *tuberosum*-ähnliche Werte erreicht. Die Merkmale der Blättchen erreichten in der BC_1-Generation Werte zwischen den Eltern (Abb. 1 und 2).

Résumé

Evaluation cytoplasmique des substitutions survenant lors des croisements en retour chez Solanum

Un programme de substitution par croisement en retour avait pour dessein de modifier les facteurs cytoplasmiques de *Solanum tuberosum* ssp. *tuberosum* dans le but d'obtenir un type qui ne présente pas de sensibilité au gène dominant de stérilité cytoplasmique.

Les facteurs de résistance cytoplasmique à la stérilité de *Solanum tuberosum* ssp. *andigena* (Juz. et Buk.) Hawkes et de *Solanum phureja* (Juz. et Buk.) ont été combinés avec les gènes de *S. tuberosum* ssp. *tuberosum* (tableau 1).

Onze caractères morphologiques de réciprocité chez les descendances F_1 et BC_1 ont été contrôlés pour évaluer le taux de régression vers les caractères parentaux de *Solanum* ssp. et pour déterminer l'influence du cytoplasme sur la forme des plantes.

La fertilité femelle et mâle des populations de F_1 et BC_1 s'avérait bonne.

Les facteurs cytoplasmiques n'ont pas beaucoup influé sur les paramètres morphologiques, à l'exception de ceux qui étaient en relation directe avec la fertilité (tableaux 6 et 7).

Les différences entre les descendances réciproques dépendaient plus des gènes de chacun des parents utilisés dans les croisements que des origines cytoplasmiques (tableaux 2–5). Aucune différence réciproque importante n'a été observée pour les caractères du tubercule et celles qui apparaissent semblaient plus dépendre de l'influence maternelle que du cytoplasme (tableaux 2–5).

Les descendances F_1 et BC_1 renfermant les facteurs de résistance cytoplasmique à la stérilité provenant de ssp. *andigena* et *S. phureja* avaient un taux de fertilité plus grand que les descendances réciproques ayant du cytoplasme de ssp. *tuberosum* (tableaux 6–7). La distribution des F_1 et BC_1 au niveau de tous les caractères morphologiques étudiés pour représenter les parents, traduisait leur nature polygénique. L'angle des feuilles et les folioles intermédiaires montraient une dominance des gènes *tuberosum* (fig. 3) tandis que les caractères présentés par les folioles étaient en rapport avec la dominance des gènes *andigena* (fig. 1 et 2). Le taux de régression vers ssp. *tuberosum* était rapide pour l'angle des feuilles et le nombre des folioles intermédiaires (fig. 3) chez les F_1, comparativement aux valeurs de *tuberosum*. Les caractères habituels des folioles étaient donnés par la valeur moyenne des parents pour les BC_1 (fig. 1 et 2).

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