

Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 1. Detection of an S locus inhibitor (Sli) gene

Kazuyoshi Hosaka¹ & Robert E. Hanneman, Jr.²

¹ Experimental Farm, Kobe University, 1348 Uzurano, Kasai, Hyogo 675-21, Japan; ² USDA, Agricultural Research Service, Vegetable Crops Research Unit, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin, 53706, U.S.A.

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Summary

A self-compatible (SC) variant of a wild diploid potato species, *Solanum chacoense*, which is normally self-incompatible (SI), was investigated for the nature and genetics of self-compatibility. It was crossed with a SI cultivated diploid potato species, *S. phureja*. The F₁ progeny segregated SC vs. SI. Diallel crosses were made among 15 F₁'s. Self-compatibility was tested in a selfed family of a parental SC variant and in sib-mated and selfed families of F₁ progeny. All the data suggest that there is a single dominant gene (Sli) with sporophytic action inhibiting S gene expression in the pollen. Plants having a 'Sli' gene, produce pollen which is compatible to its own parent and plants with similar S genes. The 'Sli' gene has been maintained in a heterozygous condition through eight selfing generations (S₈) implying that dominant homozygotes might be associated with lethality.

Introduction

Most diploid potato species (tuber-bearing *Solanums*) are self-incompatible (SI) (Swaminathan & Howard, 1953; Hawkes, 1958, 1990). The incompatibility reaction is determined by the haploid S genotype of the pollen grain (gametophytic self-incompatibility). The S alleles are co-dominantly expressed in the style, where they prevent fertilization by pollen of the same S genotype (Pushkarnath, 1942; Pandey, 1962; Cipar et al., 1964a; Thompson & Kirch, 1992). Although the gametophytic self-incompatibility system is a general rule, the occurrence of self-compatible (SC) plants within SI species has often been described. Cipar et al. (1964b) screened 11 SI species for self-compatibility and found SC variants in *S. chacoense*, *S. goniocalyx*, *S. kurtzianum*, *S. neohawkesii*, *S. phureja*, *S. pinna-tisectum*, *S. raphanifolium*, *S. sanctae-rosae*, and *S. stenotomum*. SC variants were identified also in haploids from *S. tuberosum* ssp. *tuberosum* (De Jong & Rowe, 1971; Olsder & Hermesen, 1976) and in hybrids between *S. phureja* and haploids of *S. tuberosum* ssp. *andigena* (Cipar, 1964).

Besides its breeding importance (Hawkes, 1990), *S. chacoense* Bitt. ($2n = 2x = 24$), a wild diploid potato species, represents ideal plant material to investigate genetic conversion from SI to SC. *S. chacoense* is highly SI controlled by a single S locus (Pal & Pushkarnath, 1942). Pushkarnath (1942), however, found that four of eight *S. chacoense* clones were SC. Cappadocia et al. (1986) found *S. chacoense* SC variants among androgenetic homozygous diploid plants derived from anther culture. S allele-associated pistil proteins (S proteins) have been identified in *S. chacoense* and their cDNAs were cloned and sequenced (Xu et al., 1990a, b; Després et al., 1994).

Hanneman (1985) found SC plants in *S. chacoense*, and continued selfings to S₇ generation. In this paper, genetic analysis on self-compatibility was done using interspecific F₁ and F₂ populations. In a subsequent paper, the location of the gene controlling self-compatibility in the potato genome using DNA markers will be described.

Table 1. Diallel crosses among 15 F₁ *S. chacoense* (chc 525-3) × *S. phureja* (1.22) plants (berries/pollinations). The average number of seeds per berry is given in parenthesis. Selfings are shown in bold

Female	Male															
	F ₁ -1	F ₁ -4	F ₁ -5	F ₁ -8	F ₁ -9	F ₁ -10	F ₁ -11	F ₁ -3	F ₁ -6	F ₁ -7	F ₁ -12	F ₁ -13	F ₁ -14	F ₁ -15	F ₁ -16	
F ₁ -1	10/27 (116)	0/8	1/2 (131)	0/0	1/2 (74)	0/2	0/0	0/3	0/5	0/5	0/5	0/0	0/0	3/4 (150)	2/4 (100)	
F ₁ -4	0/8	8/9 (102)	1/2 (226)	0/0	0/3	2/2 (201)	4/5 (270)	0/3	0/9	0/8	0/5	0/5	0/5	0/3	1/2 (111)	
F ₁ -5	1/5 (32)	0/2	6/9 (190)	1/3 (37)	0/2	2/7 (86)	1/4 (127)	0/6	0/4	0/1	0/4	0/7	0/6	0/5	1/7 (54)	
F ₁ -8	0/0	0/2	1/2 (93)	5/12 (84)	1/3 (44)	3/6 (108)	5/9 (156)	0/2	0/6	0/2	0/3	0/0	0/0	0/0	0/2	
F ₁ -9	0/0	3/3 (63)	2/3 (129)	1/4 (55)	12/12 (105)	2/2 (140)	2/4 (158)	0/3	0/2	0/5	0/4	0/0	0/0	0/0	0/0	
F ₁ -10	1/2 (192)	2/3 (95)	1/2 (178)	3/6 (201)	1/9 (138)	20/21 (284)	3/5 (292)	3/5 (292)	3/5 (175)	1/6 (26)	2/7 (55)	0/5	2/2 (391)	0/6	0/0	
F ₁ -11	1/4 (104)	2/2 (73)	1/3 (78)	1/6 (41)	0/0	0/0	20/23 (251)	2/2 (188)	2/3 (148)	0/4	0/0	0/0	0/0	0/0	0/0	
F ₁ -3	1/5 (66)	0/3	0/0	2/3 (138)	3/3 (61)	0/0	4/4 (188)	0/20	0/0	0/0	0/5	0/2	0/5	0/4	4/5 (128)	
F ₁ -6	1/1 (79)	1/4 (68)	2/2 (203)	1/2 (158)	1/1 (48)	0/0	2/2 (170)	0/2	0/14	0/8	0/5	0/7	0/5	0/3	1/2 (101)	
F ₁ -7	3/4 (62)	1/2 (57)	0/0	0/0	0/0	0/0	0/0	0/3	0/5	0/9	0/5	0/5	0/0	0/0	1/3 (77)	
F ₁ -12	3/6 (75)	4/7 (125)	3/6 (183)	2/9 (60)	0/3	0/3	0/3	0/5	0/5	0/9	0/30	0/5	0/5	0/4	1/4 (109)	
F ₁ -13	1/8 (44)	1/5 (74)	2/7 (88)	0/0	0/2	2/2 (50)	3/3 (154)	0/4	0/5	0/5	0/8	0/17	0/9	0/8	4/7 (53)	
F ₁ -14	0/10	1/6 (183)	2/2 (179)	1/2 (60)	0/2	0/0	2/6 (364)	0/6	0/5	0/8	0/5	0/6	0/17	0/2	0/3	
F ₁ -15	1/1 (45)	2/2 (43)	2/3 (77)	2/3 (34)	1/5 (35)	1/2 (45)	3/5 (76)	0/0	0/7	0/8	0/6	0/2	1/2 (85)	0/16	0/10	
F ₁ -16	3/5 (115)	5/8 (83)	3/5 (163)	0/0	4/5 (75)	2/2 (77)	6/7 (184)	2/6 (83)	2/6 (113)	0/5	1/4 (182)	1/2 (48)	3/5 (184)	0/8	0/14	

Materials and methods

The highly inbred line (chc 525-3) was obtained through selfing in each generation to S₇ from a SC variant of *S. chacoense* (Hanneman, 1985). It was crossed as a female with a cultivated diploid species *S. phureja* (clonal identity of 1.22). The derived 15 hybrid progeny (clonal identity of F₁-1, and F₁-3 through F₁-16) were crossed with each other and self-pollinated. F₂ families were derived by selfing F₁-10 (88H6 and 88H9 families) or sib-mating F₁-16 with F₁-6 (88H5 family) and F₁-10 with F₁-6 (88H7 family). The SC parent, chc 525-3, was selfed resulting in an S₈ population (90H23 family). All these families were characterized for self-compatibility.

Plants, except for those of the 90H23 family, were grown in pots and pollinated in an insect-free screen-

house or greenhouse. Some genotypes were highly fertile and set berries without artificial pollination. This was probably because natural pollination occurred by physical touch between anthers and stigma in an open flower during watering and handling the plants. In some genotypes, pistils were exposed outside the flower bud before anthesis. Thus, for pollinations, anthers and petals were removed from flower buds one day prior to opening, and pollen was immediately applied to the pistils. Freshly collected pollen or that stored in a desiccator in a refrigerator for no longer than two weeks was used for pollinations. The plants of the 90H23 family were selfed using the cut-stem technique (Peloquin & Hougas, 1959). Inflorescences on 20–30 cm cuttings were collected from field-grown plants and placed in water-filled bottles in a plastic

Table 2. Summary of the results of diallel crosses among F₁ *S. chacoense* (chc 525-3) × *S. phureja* (1.22) plants based on their proposed genotypes

	Female	Male	Self-compatible						Self-incompatible							
			S ₁ S ₂ Sli-					S ₁ S ₃ Sli-		S ₁ S ₂ --						
			F ₁ -1	F ₁ -4	F ₁ -5	F ₁ -8	F ₁ -9	F ₁ -10	F ₁ -11	F ₁ -3	F ₁ -6	F ₁ -7	F ₁ -12	F ₁ -13	F ₁ -14	F ₁ -15
Self-compatible	S ₁ S ₂ Sli-	F ₁ -1	+	—	+		+				—	—	—			+
		F ₁ -4	—	+	+			+	+		—	—	—	—	—	+
		F ₁ -5	+		+	+		+	+	—				—	—	+
		F ₁ -8			+	+	+	+	+		—					
		F ₁ -9		+	+	+	+	+	+			—				
	S ₁ S ₃ Sli-	F ₁ -10	+	+	+	+	+	+	+	+	+	+	+	—	+	—
		F ₁ -11	+	+	+	+			+	+	+					
	S ₁ S ₂ --	F ₁ -3	+			+	+		+	—			—		—	+
		F ₁ -6	+	+	+	+	+		+		—	—	—	—	—	+
		F ₁ -7	+	+							—	—	—	—	—	+
		F ₁ -12	+	+	+	+				—	—	—	—	—	—	+
		F ₁ -13	+	+	+			+	+		—	—	—	—	—	+
Self-incompatible	S ₁ S ₂ --	F ₁ -14	—	+	+	+			+	—	—	—	—	—	—	
		F ₁ -15	+	+	+	+	+	+	+	—	—	—			+	—
		F ₁ -16	+	+	+		+	+	+	+	+	—	+	+	+	—
	S ₁ S ₃ --	F ₁ -15	+	+	+	+	+	+	+						+	—
		F ₁ -16	+	+	+		+	+	+	+	+	—	+	+	+	—

+ = compatible, — = incompatible (at least five pollinations made, but no berry set).

S₁S₂ and S₁S₃ = assumed S locus genotypes, Sli- and -- = S locus inhibitor locus genotypes.

house. Pollinations were made on unopened flowers similar to those of pot-grown plants.

In this study, all the berries collected, except for those from the 90H23 family, contained abundant seeds; thus, the plants that set berries were regarded as SC. The plants, that did not set berries with at least nine flowers used in each selfing attempt, were regarded as SI. Segregation ratios of SC vs. SI plants were tested against expected ratios from postulated genotypes using Chi Square. In the diallel crosses made among F₁ hybrid progeny, an unsuccessful cross was noted when at least five pollinations failed.

Results

Fifteen interspecific hybrid plants were established from a cross between a SC clone of *S. chacoense* and a SI clone of *S. phureja*. Eight of them (F₁-3, F₁-6, F₁-7, F₁-12, F₁-13, F₁-14, F₁-15, and F₁-16) did not set berries upon selfing and were designated as SI. Seven plants (F₁-1, F₁-4, F₁-5, F₁-8, F₁-9, F₁-10, and F₁-11) set berries on 37% to 100% of self-pollinations, and produced an average of 191 seeds per berry, ranging from 84 to 284 (Table 1). These were designated as SC.

A total of 761 flowers were pollinated in 172 out of 210 possible combinations among F₁ hybrid progenies,

in which 88 cross combinations set berries (Table 1). In the crosses between SC plants, 36% of pollinations set berries containing an average of 143 seeds per berry. When the pollen of SC plants were applied to SI plants, 50% of pollinations set berries containing an average of 134 seeds. In the crosses of SI plants as males, berries set contained an average of 138 seeds, ranging from 26 to 391 seeds per berry. These indicate that the SI plants also had sufficient female and male fertility.

The diallel crossing results are summarized in Table 2. The crosses with SC plants as males were successful, except in three combinations. Thus, the SC plants were all crossable to both SC and SI plants. In the crosses using SI plants as males, the hybrid progeny were separated to two inter-compatible groups. F₁-1, F₁-3, F₁-4, F₁-5, F₁-6, F₁-7, F₁-8, F₁-9, F₁-12, F₁-13, and F₁-14 were all cross-incompatible with the subset of SI (F₁-3, F₁-6, F₁-7, F₁-12, F₁-13, and F₁-14), but cross-compatible with the other subset of SI (F₁-15 and F₁-16). In contrast, the rest of the hybrid progeny (F₁-10, F₁-11, F₁-15, and F₁-16) were cross-compatible with the first SI subset, but cross-incompatible with the second SI subset. The crosses between incompatible combinations never set berries, while those of possibly compatible combinations incidentally failed to set berries (Table 2).

In the 90H23 family consisting of 60 selfed progeny of chc 525-3, 20 plants (33%) could not be tested

Table 3. Self-pollinations (seeds/berries/pollinations, S/B/P) in the family 90H23, selfed progeny of chc 525-3

Plant	S/B/P	Plant	S/B/P
90H23-3	0/0/61	90H23-30	0/5/15
90H23-4	1/16/47	90H23-31	2/12/23
90H23-5	3/14/38	90H23-32	0/0/2
90H23-7	133/17/29	90H23-33	0/0/96
90H23-8	0/7/85	90H23-35	0/0/26
90H23-9	0/4/41	90H23-36	0/12/46
90H23-10	0/0/3	90H23-39	0/4/18
90H23-11	0/3/48	90H23-42	31/13/17
90H23-12	2/10/30	90H23-43	0/0/18
90H23-13	0/0/16	90H23-46	4/10/15
90H23-16	18/2/28	90H23-47	0/15/33
90H23-18	5/9/22	90H23-49	0/7/12
90H23-19	37/6/36	90H23-50	0/2/22
90H23-20	23/2/3	90H23-51	28/10/19
90H23-22	0/0/12	90H23-52	0/0/9
90H23-23	0/0/20	90H23-55	23/10/18
90H23-24	0/1/16	90H23-56	128/16/19
90H23-27	61/15/22	90H23-57	0/15/22
90H23-28	0/28/61	90H23-58	5/14/40
90H23-29	69/11/14	90H23-60	0/10/15

because of slow growth, no flowering, or no pollen shedding. Thirty of 40 plants tested set berries, while 8 failed with over 9 pollinations in each selfing attempt (Table 3). Seventeen plants produced seeds with a range from 0.06 to 11.5 per berry. Extremely low number of seeds, or often no seed, was noted. The segregation ratio of 30 berry-setting plants : 8 non-berry-setting plants fit an expected segregation ratio, whereas that of 17 seed-producing plants : 21 non-seed-producing plants was greatly skewed (Table 4). Although a critical segregation ratio of SC vs. SI could not be estimated, it is assumed that the gene controlling self-compatibility is still segregating in the S_8 population.

The 88H5 family ($SI \times SI$) consisted of 91 plants, in which 29 (32%) could not be tested because of lack of flower bud formation, flower bud abortion at a young stage, or no pollen shedding. Sixty-two plants were selfed. A total of 578 flowers were pollinated with an average of 9.3 and a range of 1 to 20 flowers per plant. None of them set berries. At least 39 plants were apparently SI, because more than nine pollinations failed.

The 88H7 family ($SC \times SI$) consisted of 72 plants, in which 8 plants (11%) were not tested. Self-pollinations were made using 533 flowers of 64 plants with an average of 8.6 pollinations per plant and a

range of 1 to 19. Sixteen plants were SC, while 25 were SI. The rest of the plants were pollinated on the low number of flowers with no berry set.

The 88H6 and 88H9 families consisted of 233 plants, in which 86 plants (37%) could not be tested. A total of 1131 pollinations were made on 147 plants with an average of 7.7 pollinations per plant, ranging from 1 to 28. Thirty-five plants were SC in 88H6, and 39 in 88H9, resulting in a total of 165 berries. Fifteen plants were SI in 88H6, and 18 in 88H9. Since there was no significant difference in SC : SI segregation ratios between 88H6 and 88H9, the two populations were combined in Table 4. The remaining 40 plants were not determined for self-compatibility because enough number of pollinations was not made.

All three F_2 families fit segregation ratios, that are expected from the hypothesis of a single dominant S locus inhibitor gene with sporophytic action and active in the pollen only (Table 4).

Discussion

SC variants of *S. chacoense* were successfully selfed to the S_8 generation despite inbreeding depression in each generation (Hanneman, 1985, and this study). De Jong & Rowe (1971) studied inbreeding depression in selfed hybrids between a cultivated diploid species and US-W4, a haploid of *S. tuberosum* ssp. *tuberosum*. S_1 , S_2 and S_3 progenies exhibited decreased performance and vigor with increased inbreeding. A serious decrease was noted in the percent of flowering plants and the level of fertility, particularly of self-fertility which was 47% in S_0 , 16% in S_1 and 16% in S_2 (De Jong & Rowe, 1971). In the present study, 11 to 37% of F_2 and 33% of S_8 progenies could not be selfed because of poor flowering or no pollen shedding. Many of the berries in selfed progeny of chc 525-3 contained no seed. This is partly attributed by reduced fertility due to inbreeding depression, although unusually high temperatures (> 30 C) in the plastic house for pollinations to cut-stems prohibited normal fertilization and seed development. It is also known that the cut-stem technique promotes fruit retention, sometimes resulting in parthenocarpy (Peloquin & Hougas, 1959; Cipar et al., 1964b).

Pollinations were made one day prior to anthesis to avoid overestimation of SC plants due to high fertility leading to erroneous berry set with the pollen of the neighboring plants. It has been known that forced pollinations to young buds, i.e. bud-pollinations, in

Table 4. Segregation of SC : SI plants in a selfed family and F₂ families derived from a SC clone, chc 525-3

Family	Pedigree	Postulated cross	Observed	Expected ratio ¹ and χ^2 value
90H23	chc 525-3 selfed	S ₁ S ₁ Sli- self	30 : 8 ² 17 : 21 ³	3 : 1 ($\chi^2 = 0.32$) or 2 : 1 ($\chi^2 = 2.58$) 3 : 1 ($\chi^2 = 18.56^*$) or 2 : 1 ($\chi^2 = 8.22^*$)
88H5	F ₁ -16 × F ₁ -6 (SI × SI)	S ₁ S ₃ - × S ₁ S ₂ --	0 : 39	0 : 1
88H7	F ₁ -10 × F ₁ -6 (SC × SI)	S ₁ S ₃ Sli- × S ₁ S ₂ --	16 : 25	1 : 1 ($\chi^2 = 1.98$)
88H6 and 88H9	F ₁ -10 selfed	S ₁ S ₃ Sli- self	74 : 33	3 : 1 ($\chi^2 = 1.95$) or 2 : 1 ($\chi^2 = 0.30$)

¹ 3 : 1 and 2 : 1 segregation ratios are expected when a dominant S locus inhibitor gene 'Sli' is sporophytically expressed in the pollen. An expected ratio of 2 : 1 instead of 3 : 1 is based on linkage of 'Sli' with a recessive lethality factor (see Discussion).

² A ratio based on the number of plants setting berries.

³ A ratio based on the number of plants producing seeds.

* Indicates significant ($P < 0.01$) deviation from expected segregation.

S₁S₁, S₁S₂, and S₁S₃ = assumed S locus genotypes, Sli- and -- = S locus inhibitor locus genotypes.

incompatible crosses can sometimes result in berry set and produce a small number of seeds. However, such a possibility caused by bud-pollinations should be excluded in this study, because the number of seeds per berry in both selfing and sib-mating was as high as the normal seed set except for the crosses in 90H23 family.

To investigate the genetics of self-compatibility in chc 525-3, it was crossed with a cultivated diploid species *S. phureja*. Self-compatibility was evaluated in the F₁ hybrid progeny and the selfed or sib-mated F₂ progeny. The results can be explained by hypothesizing a single dominant S locus inhibitor gene, 'Sli', with sporophytic action and active in the pollen only (Table 4). The genotypes of the parents can be postulated to be Sli- for a SC and -- for a SI, and either Sli- or -- for the F₁ hybrids. According to the results of the diallel crosses among F₁ hybrid progeny, the SC F₁ plants (Sli-) were cross-compatible as male parents with others as the females. It is likely that the pollen produced from SI plants (--) functioned as normal pollen expressing its S genotype. The S₇ highly inbred SC parent would probably be homozygous for an S gene (tentatively shown as S₁S₁). The other parent could have had different S genes in a normal heterozygous condition (for example, S₂S₃). Thus, the S genotypes of the hybrids could be either S₁S₂ or S₁S₃. Assuming two independent loci, S₁S₂Sli-genotype is assigned to F₁-1, F₁-4, F₁-5, F₁-8, and F₁-9; S₁S₃Sli- to F₁-10 and F₁-11; S₁S₂-- to F₁-3, F₁-6, F₁-7, F₁-12, F₁-13, and F₁-14; and S₁S₃-- to F₁-15 and F₁-16. Breeding behavior between the assumed genotypes fit the results from the diallel crosses among F₁ hybrid progeny (Table 2). Thus, it is hypothesized that the dominant gene 'Sli' is independent of the S locus and functions as an inhibitor of S genes expressed sporo-

phytically in the pollen. As compatibility depends on the genotype of the pollen parent (Sli-), and neither on the gametic genotype of the pollen (Sli or -) nor on the genotype of the pistillate parent, the 'Sli' gene is expressed in a sporophytic fashion, which is different from the gametophytic one locus incompatibility system in the tuber-bearing *Solanum* species.

Cipar (1964) reported the segregation of SC vs. SI in hybrid families between a specific clone of *S. phureja* and each of four different haploids derived from *S. tuberosum* ssp. *andigena* (PI 230457). He found that SC plants were universally cross-compatible as males, and the S allele reaction remained unchanged in the females (Cipar, 1964). The nature of the self-compatibility observed by him is probably similar to that reported in this study.

Selfed progenies of chc 525-3 and F₁-10 were either SC or SI (Table 4), indicating the heterozygous nature of the 'Sli' gene. Considering the 'Sli' gene has never been fixed as a homozygote, even though it has been selfed eight times, it is suggested that lethality is associated with a 'Sli' gene homozygote. If a recessive lethal gene is tightly linked with a dominant 'Sli' gene, the 'Sli' gene homozygote would be lethal. The segregation ratio of 2 : 1 expected from the lethality hypothesis also fits the observed segregation in selfed progenies of F₁-10 (Table 4).

De Jong (1977), however, reported that hybrids between a SC inbred (derived by inbreeding hybrid progenies of a SC haploid of *S. tuberosum* ssp. *tuberosum* × a cultivated diploid species) and a SI cultivated diploid species were all SC, showing no segregation for self-compatibility. Thus, the 'Sli' gene may be found as a homozygote in some instances. The 'Sli' gene has been transferred to a cultivated diploid species, and a subsequent inbreeding experiment is under progress;

however, presently no homozygotes have been identified.

Olsder & Hermesen (1976) and Hermesen (1978a, b) conducted a detailed genetic analysis on three extremely male fertile *S. tuberosum* haploids, one (= G609) being strictly SI, and two (G254 and B16) being highly SC with abundant seed set upon selfing and universally cross-compatible as males. They postulated an S-bearing translocation not linked to the S locus, causing self-compatibility and universal cross-compatibility as males through competitive interaction in pollen between the S allele on the translocation and S alleles on the S locus. The S-bearing translocation homozygotes are predominantly lethal, only two non-lethal ones being found in the populations studied (Hermesen, 1978b). From the extensive results the genotypes of G254, B16 and G609 were concluded to be S_1S_3/S_1 , S_3S_4/S_x and S_1S_2 , respectively, in which $/S_1$ and $/S_x$ are the translocation. All other hypotheses discussed and tested by Olsder & Hermesen (1976) were cancelled by them. Their hypothesis 2 is actually similar to our hypothesis that SC plants have a heterozygous dominant inhibitor gene, which is independent of the S locus and inactivates S alleles in the pollen only. Cancelling hypothesis 2 was mainly based on the results presented in Table 1 in Olsder & Hermesen (1976).

Recently, Thompson et al. (1991) investigated Hermesen's SC plants by using stylar S-linked glycoprotein (SLG) probes and found neither extra polypeptides nor hybridizing fragments corresponding to a translocated S_1 -allele. Two possibilities were suggested: the first is a translocation of only the pollen part of the S_1 locus which consists of two tightly linked genes, a style-specific gene encoding the SLG and a pollen-specific gene. A second is generation of an inhibitor allele at a locus unrelated to S, which acts only in pollen. They mentioned that it was not possible to distinguish between the two possible origins of Hermesen's SC plants (Thompson et al., 1991).

Selfing and reciprocal backcrossing of the first inbred generation of the SC haploids G254 and B16 unambiguously resulted into SC progeny only (see Table 1 in Olsder & Hermesen, 1976). This was expected according to the S-bearing translocation hypothesis. However, according to our 'Sli' gene hypothesis all these F_2 and BC_1 populations should segregate SC : SI and indeed we found segregation in the selfed progenies of SC plants from *S. chacoense* and from the cross *S. chacoense* $\times$ *S. phureja*. Therefore, it is obvious to

conclude that different SC systems are active in the SC plants in this study and in Hermesen's SC plants.

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References

- Cappadocia, M., D.S.K. Cheng & R. Ludlum-Simonette, 1986. Self-compatibility in doubled haploids and their F_1 hybrids, regenerated via anther culture in self-incompatible *Solanum chacoense* Bitt. Theor Appl Genet 72: 66–69.
- Cipar, M.S., 1964. Self-compatibility in hybrids between Phureja and haploid Andigena clones of *Solanum tuberosum*. Eur Potato J 7: 152–160.
- Cipar, M.S., S.J. Peloquin & R.W. Hougas, 1964a. Inheritance of incompatibility in hybrids between *Solanum tuberosum* haploids and diploid species. Euphytica 13: 163–172.
- Cipar, M.S., S.J. Peloquin & R.W. Hougas, 1964b. Variability in the expression of self-incompatibility in tuber-bearing diploid *Solanum* species. Am Potato J 41: 155–162.
- De Jong, H. & P.R. Rowe, 1971. Inbreeding in cultivated diploid potatoes. Potato Res 14: 74–83.
- De Jong, H., 1977. Self-compatibility in inbred cultivated diploid potatoes. Incompatibility Newsl 8: 16–17.
- Després, C., M. Saba-El-Leil, S.R. Rivard, D. Morse & M. Cappadocia, 1994. Molecular cloning of two *Solanum chacoense* S-alleles and a hypothesis concerning their evolution. Sex Plant Reprod 7: 169–176.
- Hanneman, R.E. Jr., 1985. Self fertility in *Solanum chacoense*. Am Potato J 62: 428–429 (abstract).
- Hawkes, J.G., 1958. Significance of wild species and primitive forms for potato breeding. Euphytica 7: 257–270.
- Hawkes, J.G., 1990. The Potato: Evolution, Biodiversity and Genetic Resources. Belhaven Press, Oxford. 259 pp.
- Hermesen, J.G.Th., 1978a. Genetics of self-compatibility in dihaploids of *Solanum tuberosum* L. 2. Detection and identification of all possible incompatibility and compatibility genotypes in six F_1 's from interdihaploid crosses. Euphytica 27: 1–11.
- Hermesen, J.G.Th., 1978b. Genetics of self-compatibility in dihaploids of *Solanum tuberosum* L. 3. Lethality of S-bearing translocation homozygotes. Euphytica 27: 13–17.

- Olsder, J. & J.G.Th. Hermesen, 1976. Genetics of self-compatibility in dihaploids of *Solanum tuberosum* L. 1. Breeding behaviour of two self-compatible dihaploids. *Euphytica* 25: 597–607.
- Pal, B.P. & Pushkarnath, 1942. Genetic nature of self- and cross-incompatibility in potatoes. *Nature* 149: 246–247.
- Pandey, K.K., 1962. Interspecific incompatibility in *Solanum* species. *Amer J Bot* 49: 874–882.
- Peloquin, S.J. & R.W. Hougas, 1959. Decapitation and genetic markers as related to haploidy in *Solanum tuberosum*. *Eur Potato J* 2: 176–183.
- Pushkarnath, 1942. Studies on sterility in potatoes. 1. The genetics of self- and cross-incompatibilities. *Indian J Genet Pl Breed* 2: 11–36.
- Swaminathan, M.S. & H.W. Howard, 1953. The cytology and genetics of the potato (*Solanum tuberosum*) and related species. *Bibliographia Genetica* 16: 1–192.
- Thompson, R.D. & H.-H. Kirch, 1992. The S-locus of flowering plants: when self-rejection is self-interest. *Trends Genet* 8: 381–387.
- Thompson, R.D., H. Uhrig, J.G.Th. Hermesen, F. Salamini & H. Kaufmann, 1991. Investigation of a self-compatible mutation in *Solanum tuberosum* clones inhibiting S-allele activity in pollen differentially. *Mol Gen Genet* 226: 283–288.
- Xu, B., P. Grun, A. Kheyr-Pour & T.-H. Kao, 1990a. Identification of pistil-specific proteins associated with three self-incompatibility alleles in *Solanum chacoense*. *Sex Plant Reprod* 3: 54–60.
- Xu, B., J. Mu, D.L. Nevins, P. Grun & T.-H. Kao, 1990b. Cloning and sequencing of cDNAs encoding two self-incompatibility associated proteins in *Solanum chacoense*. *Mol Gen Genet* 224: 341–346.