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INTERSPECIFIC HYBRIDIZATION WITH THE ALLOTETRAPLOID TUBER-BEARING SOLANUM SPECIES *S. HJERTINGII* AND *S. FENDLERI*

L.J.M. van SOEST

German-Netherlands Potato Department of the Gene Bank in the Federal Research Center for Agriculture Braunschweig-Volkenrode (FAL), a cooperation between the 'Institut für Pflanzenbau und Pflanzenzüchtung der FAL', Federal Republic of Germany, and the 'Stichting voor Plantenveredeling (SVP)', the Netherlands.

Bundesallee 50, 3300 Braunschweig, F.R, Germany

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The results of interspecific crosses carried out between the allotetraploid species *Solanum hjertingii* and *S. fendleri* on one hand and tuber-bearing wild species, dihaploids and cultivated potatoes on the other are presented. No hybrids were obtained of direct crosses between *S. tuberosum* varieties and the two species, with the exception of some unthrifities and less vigorous plants from a cross between the variety Olympia and *S. hjertingii*. However, 18 three-way hybrids were produced when the variety Olympia as pistillate parent was fertilized with a pollen mixture of the cross *S. fendleri* x *S. hjertingii*. Reciprocal crosses between the two allotetraploids on the one hand and dihaploids and diploid tuber-bearing wild species on the other, resulted in sterile triploids.

The non-race specific late blight resistance of the obtained interspecific hybrids was in general high but some variation existed between the different progenies. Finally, a possible way to transfer valuable genes of series Longipedicellata (LON) species into a cultivated background will be discussed.

INTRODUCTION

The tuber-bearing species *Solanum hjertingii* Hawkes and *S. fendleri* A. Gray belong to the series Longipedicellata (LON), which includes six species, and are mainly distributed in northern Mexico (Hawkes, 1966). Species of the

series LON, such as *S. stoloniferum*, and *S. polytrichon* are known for their resistance to *Phytophthora infestans* (Niederhauser and Mills, 1953; Toxopeus, 1964; Umaerus and Stalhammar, 1969). The systematic screening of the „German-Netherlands Potato Collection” revealed that *S. hjertingii* and *S. fendleri* have high levels of non-race specific late blight resistance (Schober, 1981; van Soest and Seidewitz, 1981). *S. hjertingii* is known for the non-blackening character of the rough and cooked tuber which is often caused through mechanical damage (Firbas, 1961) and has a certain level of blackleg resistance (Munzert, personal communications). In addition Radcliffe *et al.* (1981) found high levels of resistance to the potato aphid, particularly in *S. hjertingii* but also in *S. fendleri*. The two species are therefore considered to have high potential value for potato breeding.

All the species of the series LON are tetraploids, with the exception of the triploid *S. vallis-mexici*. In addition, there is cytological evidence that they are allotetraploids (Marks, 1958; Hawkes, 1966). Most attempts to cross allotetraploid LON species directly with cultivated tetraploid species failed. Wangerheim (1954) obtained two tetraploid hybrids from the cross *S. tuberosum* x *S. stoloniferum* which proved, however, to be highly sterile. Puskarev (1937) and Ivanov (1939), cited by Prakken and Swaminathan (1952) obtained hexaploid hybrids of the same cross. In Denmark, Foldo (personal communication) obtained hybrids between *S. tuberosum* and *S. hjertingii*. Wangerheim (1954) and Ross (1966) suggest that the crossability of species like *S. stoloniferum* (2n = 48) and *S. acaule* (2n = 48) could be improved in many cases by doubling the chromosome number. However, Wangerheim (1954) mentioned that the obtained hexaploid hybrids did not flower very much, and thus further crosses were difficult. There are several reports in the literature of successful hybridization between the allotetraploid LON species and diploid tuber-bearing *Solanums* (Koopmans, 1951; Magoon *et al.*, 1962; Toxopeus, 1964; Marks, 1965; Abdalla and Ramanna, 1971). However, these crosses resulted in sterile triploids, which may be doubled to obtain allohexaploids for further breeding as Toxopeus (1964) pointed out.

Hawkes (1966) postulated for the LON species the following genome symbols: A₄B. The A₄ genome is very similar to the A₁ genome found in many diploid wild species (e. g. *S. verrucosum*) and this explains the occurrence of sterile triploids (A₁A₄B) between LON species and some diploid species. Ross (1966) reported that the pollen sterility in *S. stoloniferum* - *S. tuberosum* hybrids is due to plasmatic effects. Ramanna and Abdalla (1970) revealed that these Mexican species seem to have sensitive plasmons which sterilize the hybrid plants with male *Solanum* species from South America. They, therefore suggested using the Mexican species as males in order to avoid the involvement of their plasmons.

This article reports on the crossing experiments with the allotetraploid species *S. hjertingii* and *S. fendleri* and the non-race specific late blight resistance in some progenies.

MATERIAL AND METHODS

Cultivated potatoes, fertile dihaploids and tuber-bearing wild species were utilized in the crossing experiments.

- (a) Cultivated potatoes (2n = 48): initially 10 different varieties, later only the varieties Olympia (OLY), Apatit (APA) and a breeding population received from Foldo-LKF-Vandel-Denmark, with *S. hjertingii* in its ancestry (BGRC 28987).
- (b) Dihaploids (2n = 24): 4 different fertile hybrids obtained from van Suchtelen-SVP-Wageningen -the Netherlands (DH 265; DH 285; DH 332 and DH 333).
- (c) Wild species as listed in Table 1. In the text, the wild species names are referred to under the three-letter code system as suggested by Simmonds (1963).

Table 1. Wild species utilized in the crosses

Species	Abbreviation	Accession numbers	2n	Country of origin
Series Longipedicellata (LON)				
<i>S. hjertingii</i>	<i>hje</i>	BGRC 8091	48	Mexico
<i>S. fendleri</i>	<i>fen(1)</i>	BGRC 8088	48	Mexico
	<i>fen(2)</i>	BGRC 8090	48	Mexico
Series Tuberosa (TUB)				
<i>S. berthaultii</i>	<i>ber</i>	BGRC 18548	24	Bolivia
<i>S. microdontum</i>	<i>mcd</i>	BGRC 18503	24	Argentina
<i>S. verrucosum</i>	<i>ver</i>	BGRC 8256	24	Mexico

Crosses were carried out in the conventional way. Pollen fertility was estimated by using lactophenol acid fuchsin.

Detached leaves, i.e. the terminal leaves of plants just before flowering, were used to screen the progenies for non-race specific late blight resistance. The method is described by Hodgson (1961) and also mentioned by Schober (1981) and van Soest and Seidewitz (1981). In general, detached leaflets of populations including 2-10 plants per cross were inoculated with the pathotype mixture 1-11 and scored for resistance after 6 to 7 days. The non-race specific late blight resistance of the basic material used in the crossing experiments is summarized in Table 2.

RESULTS

CROSSING EXPERIMENTS.

The results of all crosses made are presented in a diagram (Fig. 1) and can be summarized as follows:

(1.) Direct crosses between *hje* or *fen* with *S. tuberosum* varieties are very difficult and rarely produce vigorous hybrids. Only a few hybrids were obtained out

of the cross OLY x *hje*. However, the hybrids turned out to be unthrifities or less vigorous growing plants, which were all male sterile.

Table 2. — Non-race specific late blight resistance in foliage of basic material (scale: 1 = highly resistant; 9 = highly susceptible)

Species/Variety	Laboratory test ¹⁾		Field test ²⁾	
	Scale	No. of test	Scale	No. of test
OLY	8	3	(3) low susceptibility ³⁾	
APA	2	1	(3) low susceptibility ³⁾	
BGRC 28987	9	2	—	—
<i>hje</i>	1	7	2	2
<i>fen</i> (1)	2	4	6	1
<i>fen</i> (2)	1	7	7	2
DH-265	8	3	—	—
DH-285	9	1	—	—
DH-332	9	2	—	—
DH-333	9	3	—	—
<i>ber</i>	2	2	1	1
<i>mcd.</i>	3	3	2	1

1) according to Hodgson (1961) and Schöber (1981), detached leaflets are inoculated with a suspension containing zoospores of the pathotype 1 to 11. Scale based on sporulation index.

2) according to Tazelaar (1981), whole plants are inoculated in the field with a mixture of races. Scale based on field observations.

3) according to German variety list.

(2.) Reciprocal crosses between *hje* and *fen* on the one hand and dihaploids and diploid wild species on the other, all resulted in vigorous but male sterile plants. These hybrids could not be crossed with diploids and tetraploids and must be considered as completely sterile allotriploids.

(3.) Several interspecific vigorous hybrids were obtained from the three-way cross OLY x (*fen* x *hje*). The reciprocal crosses, however, produced only parthenocarpic berries, inviable seeds, some unthrifities or plants of reduced vigour (Table 3).

Table 3 presents the results of crosses between (*fen* x *hje*) and (*hje* x *fen*) on the one hand and the varieties OLY and APA on the other. It shows that 18 three-way hybrids were obtained using OLY as female parent. With two exceptions all plants were vigorous and exhibited morphological characters of both parents (Fig. 2 and 3). Fig. 3 shows that the vigorous hybrids OLY x (*fen* x *hje*), can be separated into three morphological groups of plants:

(1) Plants resembling the cross (*fen* x *hje*), particularly in relation to the types of leaves. These plants were, however, twice as tall as the plants obtained from the cross *fen* x *hje*. Only a few of such phenotypes were obtained.

(2) True intermediates between OLY and (*fen* x *hje*).

Fig. 1. — Diagram showing results of the crossing experiments

	OLY + APA	<i>hje</i>	<i>fen</i>	dihaploids and/or <i>ber</i> , <i>mcd</i> , <i>ver</i>	<i>fen</i> x <i>hje</i>	<i>hje</i> x <i>fen</i>
varieties (10)	n.c.	—, ±	—	n.c.	see OLY and APA	see OLY and APA
OLY + APA	sf	—, ±	—	n.c.	—, ±, +s, +c [+]	—, ±
<i>hje</i>	—, ±, +c	sf	+	+s	n.c.	n.c.
<i>fen</i>	—, ±	+	sf	+s	n.c.	n.c.
dihaploids and/or <i>ber</i> , <i>mcd</i> , <i>ver</i>	n.c.	+s	+s	sf	+s	+s
<i>fen</i> x <i>hje</i>	—, ±	n.c.	n.c.	+s	sf	n.c.
<i>hje</i> x <i>fen</i>	—, ±, +s, +c, [±]	n.c.	n.c.	+s	n.c.	sf

— no berries produced; ± berries, parthenocarpic or with inviable seeds
+c berries with viable seeds, but plants unthrifty or of less vigorous growth
+s berries with viable seeds but plants mainly sterile
+ berries with viable seeds and vigorous plants, [±] most interesting hybrids
n.c. crosses not made because irrelevant
sf because selfings no information available

Table 3. — Results from reciprocal crosses between (*fen* x *hje*) and (*hje* x *fen*) combinations and the varieties Olympia (OLY) and Apatit (APA) in 1981.

Cross	Reciprocal cross							
	n	b	s	vs	n	b	s	vs
(<i>fen</i> (1) x <i>hje</i>) x OLY	62	1	4	0	35	26	42	18**
(<i>fen</i> (1) x <i>hje</i>) x APA	61	4	4	0	7	—	—	—
(<i>fen</i> (2) x <i>hje</i>) x OLY	31	0	—	—	3	—	—	—
(<i>fen</i> (2) x <i>hje</i>) x APA	19	0	—	—	2	—	—	—
(<i>hje</i> x <i>fen</i> (2)) x OLY	102	5	11	5*	7	2	0	—
(<i>hje</i> x <i>fen</i> (2)) x APA	59	3	3	1	21	—	—	—

n = number of pollinated flowers, b = berries, s = seeds.
vs = viable seeds.

* 4 plants of reduced vigour, showing abnormal growth and no flowers (disharmony of parental genomes).

** only a few plants showed abnormal growth and did not flower.

(3) Plants more resembling the variety OLY (Fig. 2). Many of the hybrids were of this type.

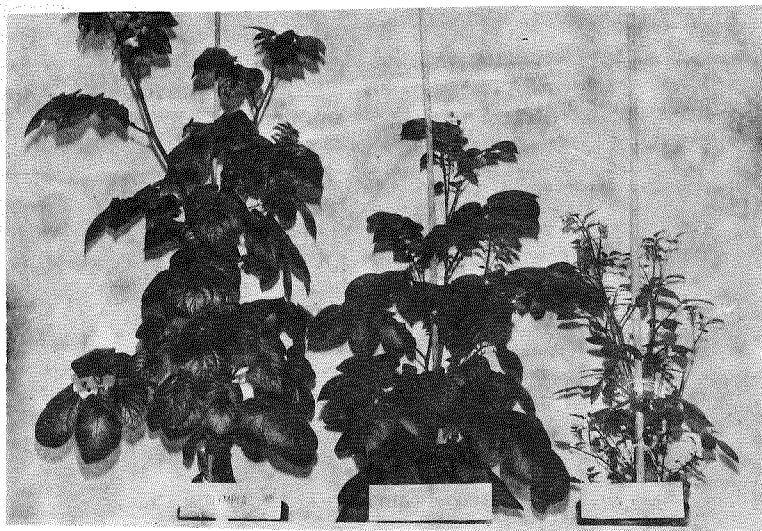


Fig. 2. Plants of the variety Olympia, the cross *fen x hje* and the three-way hybrid resembling Olympia

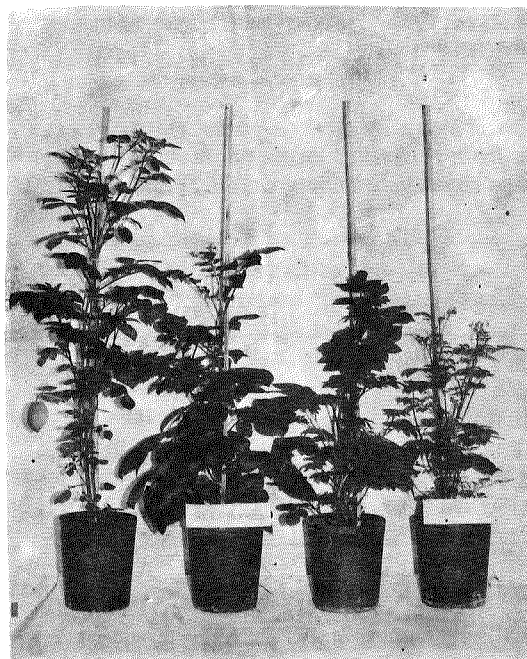


Fig. 3. Hybrid plants of the three-way cross Olympia x (*fen x hje*), three plants on the left side and the cross *fen x hje*, note the three morphological types of plants

Nearly all of the vigorous hybrids flowered but the pollen fertility was rather low. Fig. 4 shows tubers of the parents and the three-way hybrid OLY x (*fen x hje*). The three-way cross (*hje x fen*) x OLY produced five viable seeds. However, 4 plants were unthrifty and one was sterile. From a similar cross with APA, only one vigorous plant was obtained. This plant was male sterile and no hybrids could be produced using this plant as female parent.

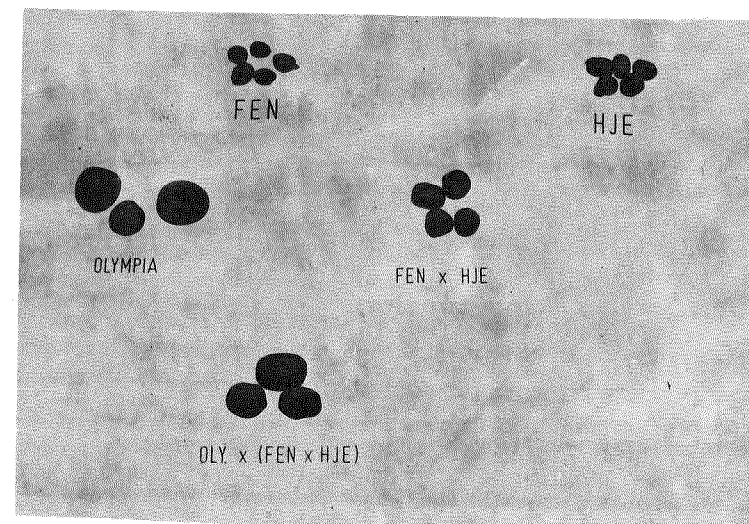


Fig. 4. Tubers of the parents and the three-way hybrid, note the size of the tubers of Olympia x (*fen x hje*)

392 crosses between 16 vigorous OLY x (*fen x hje*) hybrids as pistillate parents and OLY/BGRC 28987, produced only four viable seeds (Table 4). However, these hybrids were not obtained with the variety OLY but with the breeding population BGRC 28987 which has *hje* in its ancestry. Several parthenocarpic berries and some inviable seeds were also obtained from these crosses. Two of the four viable seeds obtained from cross (1) were unthrifty the other two seeds produced vigorous seedlings which are now grown in the greenhouse. We now need to find out, whether these plants are true hybrids and crossable with *S. tuberosum* ($2n = 48$).

NON-RACE SPECIFIC LATE BLIGHT RESISTANCE

The *Phytophthora* resistance of detached leaves of some of the progenies with *hje* and *fen* in their ancestry are summarized in Table 5. The resistance levels are somewhat variable but there is clear evidence that the resistance of both allotetraploid species is presented in the offsprings of these crosses. Remarkably high levels are found in some of the triploid progenies with the different dihaploids. This is of particular interest because all the dihaploids used are highly

Table 4. - Results of 18 hybrid plants obtained from the cross *Olympia* x (*fen* (1) x *hje*) with *Olympia* and BGRC 28987.

Cross	x	n	b	s	vs	
(1) OLY x (<i>fen</i> (1) x <i>hje</i>)	2	OLY	6	-	-	-
OLY x (<i>fen</i> (1) x <i>hje</i>)	1	28987	6	2	7	2
(2) OLY x (<i>fen</i> (1) x <i>hje</i>)	2	OLY	10	-	-	-
(3) OLY x (<i>fen</i> (1) x <i>hje</i>)	3	OLY	30	-	-	-
OLY x (<i>fen</i> (1) x <i>hje</i>)	3	28987	37	2*	-	-
(4) OLY x (<i>fen</i> (1) x <i>hje</i>)	2	OLY	16	-	-	-
OLY x (<i>fen</i> (1) x <i>hje</i>)	2	28987	6	-	-	-
(5) OLY x (<i>fen</i> (1) x <i>hje</i>)	2	OLY	21	-	-	-
OLY x (<i>fen</i> (1) x <i>hje</i>)	2	28987	23	3	1	0
(6) ^a OLY x (<i>fen</i> (1) x <i>hje</i>)	1	28987	34	8*	-	-
(7) ^a OLY x (<i>fen</i> (1) x <i>hje</i>)	1	OLY	31	-	-	-
OLY x (<i>fen</i> (1) x <i>hje</i>)	1	28987	93	-	-	-
(8) ^a OLY x (<i>fen</i> (1) x <i>hje</i>)	1	-	no	flowers		
(9) OLY x (<i>fen</i> (1) x <i>hje</i>)	1	OLY	8			
OLY x (<i>fen</i> (1) x <i>hje</i>)	3	28987	71	6	2	2

x = number of genotypes obtained from one berry. * = parthenocarpic berries.
a = to make more crosses possible these plants were vegetatively propagated.

Table 5. - Non-race specific late blight resistance of progenies of some interspecific crosses (results of laboratory test only).

Cross	2n	Scale	No. of test
<i>fen</i> (1) x <i>hje</i>	48	1	5
<i>fen</i> (2) x <i>hje</i>	48	5/6	3
<i>hje</i> x <i>fen</i> (1)	48	1	3
<i>fen</i> (1) x <i>ber</i>	36	1/2	6
<i>hje</i> x <i>ber</i>	36	2	4
<i>fen</i> x <i>mcd</i>	36	1	2
DH* x (<i>fen</i> (1) x <i>hje</i>)	36	6	4
DH 265 x (<i>hje</i> x <i>fen</i> (1))	36	1	1
(<i>fen</i> (1) x <i>hje</i>) x DH*	36	1	2
(<i>hje</i> x <i>fen</i> (1)) x DH*	36	1	2
(<i>fen</i> (2) x <i>hje</i>) x DH 285	36	5	2
OLY x (<i>fen</i> 1 x <i>hje</i>)	72?	2/3	22

*two different dihaploids
Scale: 1 = highly resistant, 9 = highly susceptible

susceptible (Table 2). The late blight resistance of all tested progenies obtained out of the cross OLY x (*fen*(1) x *hje*) is high and has on an average the scale 2/3. The non-race specific late blight resistance of the single progenies of the OLY x

Table 6. - Non-race specific late blight resistance of OLY x (*fen*(1) x *hje*) progenies (results of laboratory test only)

Progeny	No. of genotypes	Scale	Number of tests
1	3	3	3
2	2	5	2
3	3	1	3
4	2	6	3
5	2	5	2
6	1*	1	1
7	1*	1	1
8	1*	2	2
9	3	1	5

*vegetatively propagated (5 plants)
Scale: 1 = highly resistant, 9 = highly susceptible

(*fen*(1) x *hje*) crosses is presented in Table 6. The progenies 3 and 9, both including 3 genotypes showed in 3 or 5 tests, respectively, very high levels of resistance (scale 1).

DISCUSSION

In Denmark (F oldo personal communication) hybrids were produced between *hje* and *S. tuberosum*. In our experiments only a few of such hybrids, mainly unthrifities or less vigorous plants, were obtained. However, several interspecific vigorous hybrids were produced out of the three-way cross *Olympia* x (*fen* x *hje*). The chromosome numbers of these hybrids have not been counted, but most likely the plants are allohexaploids due to unreduced gametes from the male parent. This assumption agrees with the findings of Puskarev (1973), Ivanov (1939) and Hawkes (1966) who found hexaploid hybrids in crosses between *S. tuberosum* and *S. stoloniferum*. Only Wangenheim (1954) reports two tetraploid sterile plants which he found in similar crosses.

Ramanna and Abdalla (1970) suggest some degree of homology between the A₁ genome of *S. phureja* and the A₄ and B genome of *S. polytrichon*, another LON species. On the other hand they found univalents in triploid hybrids between both species. Assuming that the A₁ and A₄ genomes are more or less homologous and there is some kind of differentiation between the B genome and the A genome, there are two possible ways to obtain tetraploids out of the produced hexaploids:

- (1) Intercrosses with the hexaploids as pistillate parent and diploids (dihaploids or diploid wild species);
- (2) Intercrosses with tetraploids as males, probably once or twice to achieve tetraploids, due to chromosome elimination.

Ramanna and Hermesen (1971) reported on similar crosses with allohexaploid F₁ clones (6x - AB)² from the cross *S. acaule* x *S. bulbocastanum*.

Crosses between these hexaploids as females on the one hand and the diploid *S. phureja* and *S. tuberosum* varieties on the other showed the best results with the primitive cultivar *S. phureja*. However, most of the hybrid seeds were of bad quality and the produced hybrids had, contrary to the expectation of being tetraploids, mainly less than 48 chromosomes (Ramanna and Hermesen, 1971). In the present experiments both proposed crossing schemes were followed. So far, no seeds were obtained when the hexaploid hybrids were crossed with dihaploids and only two vigorous hybrids and two cripples were produced out of crosses with BGRC 28987, a breeding population with *hje* in its ancestry.

The results achieved are promising with respect to overcoming the first barrier in crossing LON species with *S. tuberosum*. Particularly, the utilization of (*fen* x *hje*) hybrids seems to increase the success of these crosses. This agrees with the findings of Stelzner (1943). He observed that when different accessions of the tetraploid *S. acaule*, often considered as an allotetraploid (Hermesen, 1971), were first combined, the hybrids produced could be crossed more easily with *S. tuberosum*. As most LON species can be intercrossed (Magoon and Cooper, 1959), this can be a useful approach to achieve interspecific hybridization between the LON species and *S. tuberosum*. It is thought that especially *hje* can play the function of a bridging species, as some kind of hybridization with *S. tuberosum* and this species has been found. Whether it will be possible to produce fertile tetraploids including genes of the LON species on a large scale, requires further studies.

The level of non-race specific late blight resistance of the hybrids including genes of *hje* and *fen* was in general high (Table 5 and 6). If there is some pairing in the allohexaploids between the different genomes due to some degree of homology as suggested by Ramanna and Abdalla (1970), it may be expected that some of the genes for resistance to late blight can be transferred into later generations. It is encouraging that high levels of resistance are available in several of the F₁ progenies which have genes of both LON species in their ancestry. If the late blight resistance can be transferred into potato varieties, then other valuable properties of the LON species as mentioned in this article can also be made accessible to potato breeders.

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MEĐUVRSNA HIBRIDIZACIJA SA ALOTETRAPLOIDNIM VRSTAMA
S. HJERTINGII AND *S. FENDLERI*

L.J.M. van SOEST

Nemačko-holandska gen banka za krompir, Savezni istraživački
centar za poljoprivredna istraživanja Braunschweig-Volkenrode
3300 Braunschweig, F.R. Germany

I z v o d

Prikazani su rezultati međuvrsnih ukrštanja između alotetraploidnih vrsta *Solanum hjertingii* i *S. fendleri* s jedne i divljih vrsta, dihaploida i gajenih sorata krompira s druge strane. Nisu dobijeni hibridi iz direktnih ukrštanja između sorata *S. tuberosum* i pomenute dve vrste, sa izuzetkom nekih deformisanih i manje vigoroznih biljaka iz ukrštanja između sorti Olympia i *S. hjertingii*. Međutim, dobijeno je 18 trostrukih hibrida kada je sorta Olympia korišćena kao majčinski roditelj i oprašivana smešom polena hibridne kombinacije *S. fendleri* x *S. hjertingii*. Pri recipročnom ukrštanju između ova dva alotetraploida s jedne i dihaploida i diploida divljih vrsta s druge strane, dobijeni su sterilni triploidi.

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