

Tuber yield and tuber traits of haploid-wild species F_1 hybrids

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Summary

Haploid-wild species hybrids have been produced that incorporate desirable traits and genetic diversity from wild species into the cultivated potato. Nine wild species were represented in 210 hybrids which were evaluated in a yield trial with ten haploid parents and four cultivars. Haploid-wild species hybrids yielded up to 3.1 kg/hill, compared to 1.8 kg/hill for the haploids; the species parents did not tuberize. Some $2x$ hybrids outyielded three of the $4x$ cultivars. Tubers of most hybrids, especially those with *Solanum berthaultii*, *S. canasense*, *S. cha-coense*, and *S. tarijense* as parents, were very smooth. Tuber set in many haploid-wild species hybrids was low. Extensive variability for dormancy and mass density (specific gravity) was also observed. Haploid-wild species hybrids which produce $2n$ pollen have been brought to the $4x$ level via $4x \times 2x$ crosses.

Introduction

The production of F_1 hybrids of $2x$ haploid *Solanum tuberosum*-wild species is being evaluated as a method of incorporating genetic diversity and desirable traits from wild species into the cultivated $4x$ potato. There are more than 100 wild, tuber-bearing, 24 -chromosome species which can contribute useful characteristics such as high dry matter content, low reducing sugar levels, and resistance to insects, nematodes, fungi, bacteria, viruses, drought, and frost (Hawkes, 1945, 1958; Rowe, 1969). In addition, most of the wild species are self-incompatible and, therefore, highly heterozygous. Their contribution of allelic diversity to the cultivated potato is very important to maximize heterozygosity and, thereby, obtain high tuber yields and good vigour.

Wild *Solanum* species do not normally tuberize under the long-day conditions of the north temperate region (Rudolf, 1958) and selection for tuberization in several wild species has not been very effective (Hanneman, 1979) but when the species are crossed to haploids ($2n = 2x = 24$) of *Tuberosum* cultivars ($2n = 4x = 48$), many of the $2x$ F_1 hybrid progeny do tuberize. Particular haploids have been identified as valuable parents for haploid-species hybrids that tuberize (Leue, 1983; Hermundstad & Peloquin, 1985a). Therefore, by using selected haploids, it is possible to obtain many haploid-wild species F_1 hybrids that produce tubers.

Some 2x F₁ hybrids between particular haploids and the wild, 2x species *Solanum chacoense* were reported by Leue (1983) to be very high-yielding, producing up to 2.9 kg/hill. Good tuberization was obtained in some seedlings of haploid-wild species hybrids involving several additional haploids and selections of eight other wild species parents (Hermundstad & Peloquin, 1985a). This paper reports tuber yield and tuber traits of these haploid-wild species F₁ hybrids.

Materials and methods

Crosses were made between 40 *S. tuberosum* Group Tuberosum haploids (2n = 2x = 24) as females and the following wild 2x *Solanum* species as males: *S. berthaultii* (ber), *S. boliviense* (blv), *S. canasense* (can), *S. infundibuliforme* (ifd), *S. microdonum* (mcd), *S. raphanifolium* (rap), *S. sanctae-rosae* (sct), and *S. tarijense* (tar). Of 2302 haploid-wild species F₁ plants, representing all but four of 106 families, 1397 produced tubers during the seedling generation. Of the plants that tuberized, 188 produced at least eight tubers with diameters of approximately 40 mm or more. These were entered in a yield trial along with 21 haploid-*S. chacoense* (chc) hybrids which had been previously selected for yield, ten 2x haploid parents and four 4x cultivars; tar was represented in 69 hybrids, ber in 55 hybrids, mcd in 29 hybrids, can in 18 hybrids, rap in 7 hybrids, blv and ifd in 4 hybrids each, and sct in 2 hybrids. Two replications, with two hills per replication, were planted in a randomized complete block design at each of two locations in Wisconsin, Hancock Experimental Farm and University of Wisconsin Lelah Starks Potato Breeding Farm, Rhinelander. Two tubers of each entry were planted 30 cm apart at Hancock, Wisconsin, and 50 cm apart at Rhinelander. The spacing between entries at Hancock and Rhinelander was 60 cm and 100 cm, respectively. Plants were killed after 133 days at Hancock and after 128 days at Rhinelander.

Two tubers from each clone, ca. 30 to 60 mm in diameter, were placed in moist peat moss at 15–20 °C to evaluate length of dormancy. Tubers were examined weekly and a tuber was considered to have broken dormancy if it had a sprout at least 5 mm in length.

Mass density (specific gravity) was measured on two hills of each clone with the formula:

$$\text{Mass density} = \text{tuber weight in air} / (\text{tuber weight in air} - \text{tuber weight in water}).$$

Results

Total tuber yield of many haploid-wild species hybrids was surprisingly high and greater than either parent. The yields of selected hybrids and their parents are presented in Table 1. Hybrid yield ranged from 0.0 to 3.1 kg/hill, while that of haploids was 0.2 to 1.8 kg/hill; the species did not tuberize. Hybrid yield was as much as 800 % of the high parent value. The great difference between the yield of a hybrid and its parents is illustrated in Fig. 1. Some hybrids even outyielded 4x cultivars. Tuber yields of four cultivars and the twelve highest-yielding haploid-wild species F₁ hybrids at each location are presented in Table 2. All hybrids listed outyielded the early cultivars Superior and Norland. Although no hybrid was higher-yielding than Red Pontiac, several outyielded the late cultivar Kennebec at Rhinelander. The

TUBER YIELD AND TUBER TRAITS OF HAPLOID-WILD SPECIES F₁ HYBRIDS

Table 1. Yield of selected haploid-wild species hybrids compared to parents.

Hybrid	Yield (kg/hill)			Hybrid yield as a percentage of high parent yield
	hybrid	haploid	species	
US-W4106 × tar (R) *	1.6	0.2	0	800
US-W973 × chc (R)	2.2	0.3	0	733
US-W711 × ber (H)	2.1	0.6	0	350
US-W457 × mcd (R)	1.8	0.6	0	300
US-W4837 × tar (R)	1.8	0.6	0	300
US-W2236 × can (R)	1.4	0.6	0	233
US-W973 × ifd (H)	0.8	0.7	0	114
US-W973 × rap (H)	0.2	0.7	0	29

* R = grown at – Gewachsen bei – Cultivé à Rhineland, WI; H = grown at Hancock, WI.

*Tabelle 1. Der Ertrag ausgewählter Haploid-Wildarten Hybriden im Vergleich zu den Eltern.
Tableau 1. Productions comparées des hybrides issus d'espèces haploïdes sauvages et de leurs parents.*

Fig. 1. Tuber yield, per hill, of parents and hybrid: haploid US-W973 (left), US-W973 × *S. berthaultii* (center), and *S. berthaultii* (right).



Abb. 1. Knollenertrag/Hügel der Eltern und der Hybride: Haploid US-W973 (links), US-W973 × S. berthaultii (Mitte) und S. berthaultii (rechts).

Fig. 1. Rendement en tubercules par pied des parents et hybrides: haploïde US-W973 (à gauche), US-W973 × S. berthaultii (au centre) et S. berthaultii (à droite).

Table 2. Yield of cultivars and highest-yielding haploid-wild species F_1 hybrids.

	Hancock yield (kg/hill)		Rhineland yield (kg/hill)
<i>Hybrid</i>		<i>Hybrid</i>	
US-W457 × tar	2.9	US-W3463 × mcd	3.1
US-W4139 × tar	2.5	US-W4139 × tar	2.9
US-W4837 × tar	2.5	US-W10483 × ber	2.3
US-W457 × tar	2.4	US-W3611 × ber	2.2
US-W2838 × mcd	2.3	US-W973 × chc	2.2
US-W152 × chc	2.3	US-W2838 × tar	2.2
US-W457 × tar	2.2	US-W973 × chc	2.0
US-W788 × chc	2.2	US-W3611 × ber	1.8
US-W3611 × ber	2.1	US-W4837 × tar	1.8
US-W711 × ber	2.1	US-W457 × mcd	1.8
US-W973 × ber	2.1	US-W788 × chc	1.8
US-W3328 × chc	2.1	US-W2838 × ber	1.7
<i>Cultivar</i>		<i>Cultivar</i>	
Superior	1.5	Superior	1.0
Norland	2.0	Norland	1.2
Kennebec	2.9	Kennebec	2.0
Red Pontiac	3.2	Red Pontiac	3.5

Tabelle 2. Ertrag der Sorten und der Höchstertrag-gebenden Haploid-Wildarten F_1 -Hybriden.

Tableau 2. Productions comparées des variétés et des hybrides F_1 à haut rendement issus des espèces haploïdes sauvages.

twelve highest-yielding clones at Hancock were not the same as those at Rhineland, indicating a possible genotype × environment interaction.

The majority of haploid-wild species hybrids produced large, smooth tubers. The species parent appears to be important in determining eye depth and degree of raised internode area. Hybrids in which ber, can, chc, and tar were parents produced tubers which remained smooth even when they became very large. In contrast, hybrids involving mcd tended to have deeper eyes and moderately raised internodes. The other species (blv, ifd, rap, sct) produced tubers that remained small, so tuber type was difficult to evaluate.

Tuber set was generally low in the haploid-wild species hybrids, even though tuber yield was often very high. There were fewer than 15 tubers per hill for 65 % and 80 % of the haploid-species hybrids at Hancock and Rhineland, respectively. Cultivar tuber set ranged from 11 to 14 at Hancock and 8 to 28 at Rhineland. In a particular example, the hybrid US-W3611 × ber produced 11 tubers per hill, yielding 2.2 kg while Kennebec set 19 tubers per hill to yield 2.0 kg.

There was much variation among and within families for length of tuber dormancy. For the haploid-wild species hybrids, the range was 22 to 207 days from harvest to initiation of sprouting. In contrast, the range of the haploids was 45 to 158 days and that of the cultivars was 45 to 108 days. In general, dormancy of the hybrids was

Table 3. Length of dormancy of full sib clones of two haploid-wild species hybrids.

	Clone	Number of days from harvest to 5 mm sprout		
		Tuber 1	Tuber 2	mean
US-W3463 × mcd	1	158	165	161.5
	2	87	101	94.0
	3	137	158	147.5
	4	58	58	58.0
W711 × ber	1	130	158	144.0
	2	144	158	151.0
	3	165	171	168.0
	4	182	190	186.0

Tabelle 3. Dauer der Keimruhe von Klonen gleicher Abstammung bei zwei Haploid-Wildarten Hybriden.

Tableau 3. Longueur de la dormance de clones apparentés de deux hybrides issus d'espèces haploïdes sauvages.

longer than that of the four cultivars but not necessarily of the haploids. There were many haploid-species hybrids in which some clones had long dormancy while some of their full sibs had short dormancy. For example, among full sibs of US-W3463 × mcd, two clones sprouted less than 100 days after harvest and two clones took ca. 150 days to break dormancy (Table 3). With other crosses, such as W711 × ber, all full sibs, had a long dormancy period.

Mass density also varied greatly among haploid-wild species clones. The range extended from 1.050 for a US-W2838 × tar hybrid and a US-W457 × tar hybrid to 1.110 for a US-W2236 × tar hybrid. This compares to a range of 1.058 to 1.079 for the haploids and 1.051 to 1.076 for the cultivars. Mass density measurements above 1.085 were obtained for 30 of the hybrids.

Discussion

The production of haploid-wild species hybrids is a very effective method of utilizing wild species germplasm. It puts unadapted material into a form which will tuberize. This is important for two reasons. First, valuable genotypes can be maintained easily, because they tuberize readily in the field. Secondly, tuber characteristics of the hybrids can be evaluated, making it possible to determine parental values of species genotypes for these traits. There were differences in tuber traits attributable to the species parents, for example, ber, tar, and can produced hybrids with large, smooth tubers, while tubers of mcd were smaller and rougher. In the future it should be possible to screen plants from introductions of many species for their contribution of desirable tuber traits as well as other important characteristics.

It is interesting to compare tuber characteristics of haploid-wild species hybrids with those of Group Phureja (a cultivated diploid) – haploid hybrids, although direct comparisons have not been made in this experiment. Extensive experience with

Phureja-haploid hybrids indicates that their tubers are usually less desirable than those of haploid-wild species hybrids for several traits. Most Phureja-haploid hybrids produce numerous tubers that are rough because of their deep eyes and raised internodes, are variable in size, and have short dormancy (Schroeder, 1983). In contrast the tubers of haploid-wild species hybrids, especially those involving ber and tar, are usually few in number, smooth and uniform in size, dormancy varying with genotype, from short to very long.

Several 2x haploid-wild species hybrids outyielded 4x cultivars. Although the hybrids were undoubtedly high-yielding, they may have been given an advantage over the cultivars because all tubers were planted at a much wider spacing than that of customary agricultural practice. (A yield trial with selected haploid-wild species hybrids planted at 30 cm spacing is currently being conducted.) Moreover, because tubers were harvested ca. 130 days after planting, the early cultivars Norland and Superior were penalized and they probably would have ranked much higher if there had been a 90-day harvest.

The very high tuber yield of many of the haploid-species hybrids reflects the importance of genetic diversity in potato. It is generally believed that the 4x cultivated potato has a relatively narrow germplasm base (Howard, 1970; Mendoza & Haynes, 1974) and that heterozygosity is necessary for high yield (Rowe, 1967; Mendiburu, Peloquin & Mok, 1974). The wild potato species can make an important contribution of allelic diversity to the Group Tuberosum. However, this contribution is valuable only if it is incorporated into adapted germplasm where it will be reflected by high tuber yields. The importance of haploids in the utilization of wild species should, therefore, be emphasized.

Genetic variability within and among both haploid and species parents results not only in heterozygous, but also in heterogeneous hybrid progeny and this variability can be very useful in genetic studies. For example, the clones with large differences in tuber set would be useful in a study of the genetic control of tuber number.

Haploid-wild species hybrids also provide valuable material for potato breeding programmes. Several of the hybrids produce 2n pollen (Hermundstad & Peloquin, 1985b) and have been crossed as males to tetraploids, producing tetraploid progenies via unilateral sexual polyploidization (USP). Reports of significant yield heterosis after $4x \times 2x$ crosses, where the 2x parent is a haploid-chc or Phureja-haploid hybrid, verify that USP is a valuable breeding scheme (Hanneman & Peloquin, 1969; Mok & Peloquin, 1975; DeJong & Tai, 1977; Mendiburu & Peloquin, 1977a; McHale & Lauer, 1981; Masson, 1985). 2n gametes are an important component of USP because they effectively transmit intra- and inter-locus interactions from the 2x hybrid to the 4x level. An even greater proportion of these interactions is transmitted intact if both parents are 2x and produce 2n gametes via a first division restitution mode (Mendiburu et al., 1974). Some of the resulting progeny would be 4x products of bilateral sexual polyploidization (BSP). This method was proposed in Chase's (1963) outline of an analytic breeding scheme. Tetraploid progeny of $2x \times 2x$ crosses involving phu-haploid and/or haploid-chc hybrids are generally vigorous and outyield their 2x full sibs (Mendiburu & Peloquin, 1977b; Chujoy, 1983). The 2x progeny of these $2x \times 2x$ crosses are also valuable as highly heterozygous parents of USP and BSP breeding schemes.

It is encouraging that many of the haploid-species hybrids produced to date possess good tuber traits together with high yield potential. Therefore, acceptable tuber

quality in material containing wild species germplasm should not be difficult to obtain.

Potato breeders are fortunate to have a very large amount of genetic diversity available to them in the form of wild species. The use of haploid-species hybrids provides a method which will make this valuable material more readily accessible to breeders by putting it into a form which is easy to handle and incorporate into a breeding programme.

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Zusammenfassung

Knollenertrag und Knollenmerkmale von Haploid-Wildarten F_1 -Hybriden

Es wurden Haploid-Wildarten F_1 -Hybriden erzeugt, um aus Wildarten in Zuchtkartoffeln wünschenswerte Merkmale und genetische Mannigfaltigkeit hineinzubringen. Vier Sorten, zehn Haploide und 210 Haploid-Wildarten F_1 -Hybriden, einschliesslich der folgenden 2x-Wildarten, wurden in einen Ertragsversuch einbezogen: *S. berthaultii* (ber), *S. boliviense* (blv), *S. canasense* (can), *S. cha-coense* (chc), *S. infundibuliforme* (ifd), *S. microdontum* (mcd), *S. sanctae-rosae* (sct), *S. raphanifolium* (rap), and *S. tarijense* (tar).

Die Erträge vieler Haploid-Wildarten Hybriden waren erstaunlich hoch, bis zu 3,1 kg/Hügel und grösser als bei jeweils beiden Eltern (Tabelle 1). Haploide ergaben bis zu 1,8 kg/Hügel, die Arten-Eltern bildeten keine Knollen. Die Abb. 1 veranschaulicht den Unterschied zwischen dem Ertrag einer Hybride und ihrer Eltern. Einige 2x-Hybriden übertrafen 4x-Sorten (Tabelle 2): Grössere Pflanzweiten und eine lange Wachstumszeit mögen den Hybriden einen Vorteil gegenüber den Sorten gegeben haben. Die Knollen der meisten Haploid-Wildarten Hybriden waren sehr weich, besonders diejenigen mit ber, can, chc und tar als Eltern.

Bei einigen Haploid-Wildarten Hybriden

hatten alle Klone gleicher Abstammung eine lange Knollenkeimruhe, bei anderen waren einige Klone innerhalb der gleichen Abstammung mit langer, andere mit kurzer Keimruhe (Tabelle 3).

Die Massendichte (spezifische Gewicht) variierte innerhalb der Haploid-Wildarten Hybriden von 1,050 für eine US-W2838 $\times$ tar Hybride und eine US-W457 $\times$ tar Hybride bis 1,110 für eine US-W2236 $\times$ tar Hybride; Haploide variieren von 1,058 bis 1,079 und Sorten von 1,051 bis 1,076.

Die Erzeugung von Haploid-Wildarten Hybriden ist eine wirkungsvolle Methode, um nicht adaptiertes Wildarten-Erbgut in eine Form zu bringen, die Knollen ausbilden wird.

Dies erlaubt die leichte Erhaltung wertvoller Genotypen und die Abschätzung der Beiträge von Wildarten-Genotypen zum Ertrag und zu den Knollenmerkmalen. Auch erhält man damit ein hoch variables Material für genetische Untersuchungen. Haploid-Wildarten Hybriden, die 2n-Pollen erzeugen, wurden in 4x $\times$ 2x Kreuzungen verwendet, um 4x-Hybriden herzustellen, die in Kartoffelzuchtprogrammen eingesetzt werden können.

Résumé

Production et caractéristiques des tubercules d'hybrides F_1 issus d'espèces haploïdes sauvages

Des hybrides F_1 issus d'espèces haploïdes sauvages ont été produits dans le but d'introduire des caractères désirables et la diversité génétique dans les pommes de terre cultivées. Quatre variétés, dix haploïdes et 210 hybrides F_1 issus d'espèces haploïdes sauvages, incluant les espèces sauvages $2x$, entraient dans l'essai de productivité: *S. berthaultii* (ber), *S. boliviense* (blv), *S. canasense* (can), *S. chacoense* (chc), *S. infundibuliforme* (ifd), *S. microdontum* (mcd), *S. sanctae-rosae* (sct), *S. raphanifolium* (rap) et *S. tarijense* (tar). La production de nombreux hybrides issus d'espèces haploïdes sauvages était notablement élevée, plus de 3.1 par pied, et plus forte que celle de leurs parents (tableau 1). Les haploïdes produisaient 1.8 kg/pied; les espèces parentales ne tubérisaient pas.

La figure 1 illustre les différences observées entre le rendement de l'hybride et celui de ses parents. Quelques hybrides $2x$ surpassaient les variétés $4x$ (tableau 2). Un espacement important et une longue durée de végétation pourraient avoir donné un avantage aux hybrides sur les variétés. Les tubercules de la plupart des hybrides issus d'espèces haploïdes sauvages, notamment de ceux dont les

parents étaient ber, can, chc et tar, étaient lisses. Quelques hybrides d'espèces haploïdes sauvages, tous apparentés, présentaient une longue dormance; pour d'autres la dormance était courte (tableau 3). Parmi les hybrides issus d'espèces haploïdes sauvages, la densité (le poids spécifique) variait de 1.050 pour US-W2838 $\times$ tar et US-W457 $\times$ tar à 1.100 pour US-W2236 $\times$ tar; les haploïdes s'échelonnaient de 1.058 à 1.079 et les variétés de 1.051 à 1.076.

La production d'hybrides à partir d'espèces haploïdes sauvages est une méthode efficace pour introduire le caractère tubérifère chez des espèces sauvages qui ne le sont pas. Elle permet la maintenance facile de génotypes valables et l'évaluation de l'apport des génotypes d'espèces sauvages au rendement et aux caractéristiques des tubercules. Elle fournit aussi un matériel hautement variable pour les études génétiques. Des hybrides issus d'espèces haploïdes sauvages produisant du pollen $2n$ étaient utilisés dans les croisements $4x$ et $2x$ pour obtenir des hybrides $4x$ qui pourront contribuer aux programmes d'hybridation de la pomme de terre.

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