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Selection inherent in monoploid derivation mechanisms for potato

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Abstract Monoploid potato (2n=1×=12) can be derived either paternally through anther or microspore culture (androgenesis) or maternally through crossing with a haploid-inducing pollinator (gynogenesis). Androgenic and gynogenic monoploid populations, derived from each of two *Solanum phureja* clones, were compared in both greenhouse and field studies, and their frequency of cells at the 1*x*, 2*x* and 4*x* DNA contents was estimated by flow cytometry of in vitro plantlets. In 15 of 17 comparisons of morphological data (plant height, number of main stems, vigor, leaf length and width, internode length, tuber number and tuber weight) where a significant difference was found due to derivation, the androgenic monoploids were agronomically superior to their gynogenic counterparts (13–18% greater leaf size, double to triple the total tuber yield). Only plant height was significantly greater (26–27%) in the gynogenic monoploids. Flow cytometry revealed that the gynogenic monoploids retained 5% more cells at the monoploid level, whereas androgenic monoploids exhibited 27% more endopolyploid cells at the tetraploid level.

Keywords Androgenesis · Endopolyploidization · Gynogenesis · Haploid · *Solanum phureja*

Introduction

The ability to generate haploid progeny through anther culture and various gynogenic mechanisms in many species has been heralded as a means to increase efficiency and precision in genetic studies and applied breeding programs. Through haploidization, homozygous lines of any responsive crop, inbreeding or outcrossing, can be produced in a single generation. In self-pollinating crops, these homozygous lines were envisioned as fully developed cultivars; in hybrid production as breeding lines to be test-crossed; and in strictly out-crossing crops, which breed at a hemizygous level, as the only means to eliminate deleterious recessive alleles and produce uniform, highly heterozygous hybrids through the selection and combination of doubled-haploids (Wenzel et al. 1979). Haploids are now extensively utilized in the development of homozygous lines of maize, barley, wheat, rice and canola.

In some applications, haploids have met or even exceeded their expectations. Murigneux et al. (1993) found that maize lines derived through anther culture were as vigorous as those derived through single-seed descent. Bjornstad et al. (1993) found that barley populations derived through single-seed descent, gynogenesis and androgenesis, from each of three F_1 hybrids, exhibited different genotypic arrays. However, the best mechanism differed among the three crosses, so that no single mechanism was consistently favored (Bjornstad et al. 1993).

In tobacco, Burk and Matzinger (1976) found a reduced yield of doubled-haploids compared to the source inbred cultivar. Schnell et al. (1980) concluded that single-seed descent was superior to androgenesis in tobacco because the yield of the best line derived through single-seed descent was greater than that of the best anther-derived line. A comparison of androgenic and gynogenic doubled-haploids and selfed progeny derived from a doubled-haploid tobacco plant revealed that the gynogenic monoploids and selfed progeny were equivalent, but that the androgenic lines were highly variable and generally reduced in vigor (Kumashiro and Oinuma 1985). Therefore, the haploid state itself was not detrimental; rather, androgenesis must impose some modification upon the regenerants. Brown et al. (1983) reported that a second cycle of anther culture reduced the yield of tobacco doubled-haploids additionally by 15–17%, even after the first cycle of doubled-haploids already exhibit-

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ed a yield reduction of 12–18% over that of the inbred line used as a source of anthers.

In *Nicotiana sylvestris*, anther-derived lines displayed an abnormal phenotype and a reduced growth that was transmitted to successive selfed generations (De Paepe et al. 1981). The authors suggested that differences between the generative and vegetative nuclei gave rise to this systematic mutation that increased in additional cycles of androgenesis. *Nicotiana tabacum* doubled-haploids exhibited a mean increase in heterochromatin of 12% over the parental value. The nuclear DNA content of the doubled-haploids was 10.62 pg, compared to 9.32 pg for the parents (Dhillon et al. 1983).

In a cross-pollinated crop such as potato, genetic variation among doubled-haploids is expected because of the high level of heterozygosity present in the parental cultivars. This, in conjunction with inbreeding depression, complicates comparisons between source cultivars and populations of doubled-haploids. For potato breeding and genetics, one concern is whether androgenesis or gynogenesis is the preferred mechanism of haploid derivation, and another is whether haploidization induces undesirable change. Androgenesis has been suggested as the potentially superior mechanism in potato, as there are greater numbers of microspores among which superior recombinants can occur than ovules in a flower (Jacobsen and Ramanna 1994), and androgenesis is generally considered more efficient than gynogenesis (Foroughi-Wehr and Wenzel 1993). However, the success of both techniques is genetically controlled and varies widely among genotypes. In addition, more gametes do not necessarily give rise to more haploids. Efficiency is unquestionably a matter of concern when deciding upon the mechanism of haploid derivation; but, if the populations resulting from androgenesis and gynogenesis are not equivalent on both phenotypic and genotypic levels, one mechanism may be preferred over the alternative, regardless of relative efficiency. Comparisons of androgenic and gynogenic haploids have been previously reported only in crops that tolerate inbreeding. A systematic evaluation of androgenic and gynogenic monoploid populations has not been conducted in potato. Dihaploids of tetraploid *Solanum tuberosum* L. cultivars are generally weak and infertile (Ross 1986), thus presenting an obstacle in attempts to develop monoploids. The few monoploids that have been developed have been extremely weak and tuberized poorly (van Breukelen 1981; Uijtewaal et al. 1987). Therefore, we have focused the present study on monoploids of the cultivated diploid potato, *Solanum phureja* Juz. & Buk., an outcrossing species that has been used extensively in potato breeding but for which monoploids can be more readily obtained and are generally more vigorous.

Our study's broad objectives were to compare the performance of monoploid potatoes developed through androgenesis via anther culture and gynogenesis, using a haploid-inducing pollinator. Our specific objectives were to: (1) compare morphological characteristics and the general performance of androgenic and gynogenic monoploids from two *S. phureja* clones under field and greenhouse conditions; and (2) compare the DNA content of *S. phureja* androgenic and gynogenic monoploids via flow cytometry.

Material and methods

Plant material

Gynogenic monoploids were derived from cross-pollinations between each of two independently selected *S. phureja* clones, PP5 (PIs 225669 and 225682) and BARD 1–3 (PI 225669), and the haploid-inducing pollinator, *S. phureja* IVP 101 (PIs 225882 and 225702). Androgenic monoploids were derived through anther culture of PP5 and BARD 1–3 (Snider and Veilleux 1994). The monoploids were verified by flow cytometry (Owen et al. 1988) and maintained in vitro.

Greenhouse experiment 1 – PP5 derivatives

In vitro shoots of 21 androgenic and 21 gynogenic monoploids derived from *S. phureja* clone PP5 were subcultured in baby food jars containing 40 ml of 1/2-strength MS (Murashige and Skoog 1962) basal medium (0.5×MS salts, 30 g of sucrose, and 7 g of agar per liter, pH=5.8). Approximately nine three-node shoots of each clone were placed in jars with four to five shoots per jar from September 1–4, 1997, and were rooted for 3 weeks in an incubator at 21°C with fluorescent lighting (125 µmol m^{-2} sec^{-1}) and 16-h daylength. After incubation (roots approximately 1.5–4-cm long) cuttings were transferred to domed plastic flats containing potato soil mix [2 parts Sunshine mix (Sun Gro Horticulture, Inc., Bellevue, Washington):1 part sand] and were acclimated under shade cloth. The plastic covers and shade cloth were gradually removed over a 1-week period. Acclimated plants were transferred to 3.8-l pots containing potato soil mix and grown for 6 weeks. Six to nine three-node cuttings were taken from each clone, dipped in Rootone, placed into flats containing potato soil mix, and rooted under intermittent mist for 3 weeks. Three rooted cuttings were selected per clone and transplanted into 1.9-l pots of potato soil mix and grown at 15°C (night)/24°C (day). Natural lighting was supplemented with high-intensity sodium lamps to extend daylength to 16 h. The 42 clones were placed in a randomized complete block design with three replications, grown on adjacent tables in the same greenhouse.

At 30 days after planting, the following data were collected: plant height, number of main stems, and vigor based on a five-point scale (1=most vigorous; 5=dead). At 90 days, three measurements per plant on internode length and a second vigor rating were taken. The length and width of three fully expanded leaves were measured per plant. The total number of leaflets per leaf was counted for three leaves on each plant. Generally, measurements were taken on the seventh, eighth, and ninth leaves from the shoot apex of each plant. Floral data were taken on the number of buds per inflorescence. When possible, at least ten flowers of each plant were emasculated and pollinated with fresh pollen from the diploid clone ID5, kindly provided by J. Pavek, USDA/ARS, Aberdeen, Idaho. ID5 was selected as the pollen parent for its known ability to induce fruit-set in crosses with doubled monoploids derived from PP5 (Paz and Veilleux 1997). This is a complex hybrid comprising 1/2 *Solanum stenotomum* PI 195188, 3/16 *S. phureja* PI225685, 3/16 *S. tuberosum* (US-W1, US-W1711, A483–17) and 1/8 *Solanum chacoense* PI 133085. Plants were harvested on April 18, and data were taken on the number of tubers per plant, the total tuber weight per plant, the mean weight per tuber, the tuber skin color, the tuber flesh color, and the tuber appearance (rough, moderate, or smooth). Analysis of variance was performed on all data collected from the greenhouse study using JMPin version 3.0 (SAS Institute 1996).

Greenhouse experiment 2 – PP5 and BARD 1–3 derivatives

In August 1998, three copies per clone of 88 in vitro androgenic and gynogenic monoploids from both parental lines were established in the greenhouse as above. After 6 weeks, six cuttings of each of the 73 surviving monoploid clones were dipped in Rootone powder and planted in flats with plastic domes. The three most-vigorous cuttings of each clone were used for the greenhouse study initiated in December 1998. The experimental design consisted of a total of 73 monoploids (14 PP5 androgenic, 20 PP5 gynogenic, 21 BARD 1–3 androgenic, and 18 BARD 1–3 gynogenic) planted in 10-cm pots in a randomized complete block of one-plant plots in three replications under natural daylength extended to 16 h by high-intensity sodium lamps. Of the 14 and 20 PP5 androgenic and gynogenic monoploids in this study, 12 and 17, respectively, were replicated in the earlier greenhouse study.

After 1 month, data were collected on: (1) vigor on a 1–5 scale as above; (2) the number of shoots; and (3) the height in cm. After 2 months, the following data were collected: (4) terminal leaflet length and width (three fully expanded young leaves per plant); (5) leaflet number; and (6) leaf ratio: average terminal leaflet length divided by average terminal leaflet width. After 4 months: (7) internode length: the length of the third, fourth and fifth internodes from the base of the plants in cm; (8) the tuber number based on tubers greater than 5-mm diameter; (9) the total tuber weight; and (10) the average tuber weight (ATW): total yield divided by number of tubers per plant. Data were analyzed by ANOVA.

Field studies

Two field studies were conducted on androgenic and gynogenic monoploids, as tubers became available. In 1998, a study consisting of three replications of single-plant plots of ten androgenic and 11 gynogenic monoploids of PP5 was planted at the Kentland Farm, Virginia Polytechnic Institute and State University, Blacksburg. Tubers harvested from greenhouse-grown monoploids were planted in 10-cm pots in April 1998 and all clones with three plants were transplanted to the field in a randomized complete block design consisting of single-plant plots on May 21, 1998. Black landscape fabric was used to deter weed competition. The plants were harvested on August 27, 1998. The following data were taken: leaf length and width, stem number, and vigor 1 month after planting; tuber number, and total tuber weight at harvest.

In 1999, a second field study comparing androgenic and gynogenic monoploids of both families was conducted, again using tuber-propagated plants that were grown in the greenhouse and transplanted to the field on June 1, 1999. Plant emergence from greenhouse tubers was considerably less than in 1998, thereby limiting the available plant material. Rather than base the comparison on only the few clones for which we had three plants, we altered the experimental design to accommodate as many different clones as possible. We used a completely random design with unequal replication (from one to eight copies of each genotype) of 13 androgenic BARD 1–3, six gynogenic BARD 1–3, 13 PP5 androgenic (six of which were present in the 1998 field study and seven new clones), and 17 PP5 gynogenic (seven of which were present in the 1998 field study and ten new clones) monoploids. Data were collected on: vigor, stem number, height at 1 month after planting, tuber number and tuber weight at harvest (August 27, 1999).

Nuclear DNA comparison

In each of two studies comprising of 20 (ten androgenic and ten gynogenic) distinct monoploid clones derived from BARD 1–3, three in vitro plantlets per clone were subcultured for estimating DNA content. Shoots (3 cm) from in vitro plantlets were propagated in 25×150-mm culture tubes containing 18 ml of MS basal medium and placed in a 21°C incubator (75 µE s^{-1} m^{-2}) under a 16-h daylength. The plantlets were grown and analyzed in a randomized complete block design with three replications. DNA content was estimated via flow cytometry as described by Owen et al. (1988) using a Coulter Epics XL flow cytometer (Coulter International Corporation, Miami, Florida.). Data were collected on the frequencies of nuclei comprising the 1×, 2×, and 4× peaks and the peak positive values (the channel number where the highest frequency of cells was found in each peak). The analysis of variance between derivations was performed using PROC GLM (SAS Release 6.12).

Results

Greenhouse experiment 1

Of the ten traits analyzed in the PP5 monoploid families in 1998, ANOVA revealed significant differences between androgenic and gynogenic populations for four traits: plant height, leaf length and width, and total tuber weight. After 1 month, the gynogenic monoploids were significantly taller (26%) than the androgenic monoploids, with mean height for the gynogenic population at 11.6 cm compared to 9.2 cm for the androgenic population. Mean leaf length was significantly greater by 13% in the androgenic population compared to the gynogenic population (5.4 and 4.8 cm, respectively). Similarly, leaf width was significantly greater by 13% in the androgenic population (3.5 vs 3.1 cm). Mean total tuber weight per plant was significantly greater by 35% in the androgenic population (18.6 vs 13.8 g; Table 1); however, its components, mean tuber number and average tuber weight, did not differ significantly between the populations.

Tuber flesh color (yellow versus white) is controlled by a single gene (*Y*); yellow flesh is dominant to white. PP5 is known to be heterozygous (*Yy*) at the *Y* locus from a previous study (Singsit et al. 1990). Therefore, the monoploids extracted from PP5 would be expected to segregate 1:1 for yellow:white flesh. Segregation for tuber flesh color did not differ significantly from the expected 1:1 ratio in both populations combined, as determined by chi-square analysis (χ^2_1=0.88, p>0.05); 50% of the androgenic monoploids produced yellow tubers whereas 63% of the gynogenic monoploids were yellow.

Flower color, corolla width, style length, and anthers per bud could not be statistically analyzed due to missing data. Although all clones initiated floral buds, many flowers did not open and abscised prematurely or else were extremely deformed, which hampered data collection. The mean number of buds per inflorescence was 5.7 and 6.0 for the gynogenic and androgenic monoploids, respectively, and was not significantly different.

Variation among clones within a mechanism of derivation was expected, since all genotypes were random gametic samples of a heterozygous parent. Clone-within-derivation was significant at the 0.05 level for plant height, internode length, vigor, leaf length, leaf width, number of leaflets per leaf, total tuber weight, and buds per inflorescence. Replication was also significant for in-

Table 1 Means for ten phenotypic traits of androgenic (AM) and gynogenic monoploids (GM) derived from the *S. phureja* families PP5 and BARD 1–3 in greenhouse studies conducted over 2 years

Monoploid type	Vigor	Height	Shoot no	Leaf length	Leaf width	Leaflet no	Internode	Tuber no	Tuber wt	ATW
PP5 1998										
AM	2	9.2 b[a]	1.5	5.4 a	3.5 a	7.6	1.2	5.2	18.6 a	4.6
GM	2	11.6 a	1.6	4.8 b	3.1 b	7.3	1.3	4.9	13.8 b	4.0
PP5 1999										
AM	1.7	19.9	2.5	2.7 a	1.6 a	10.9	9.3	2.9	6.5	2.9
GM	1.8	21.0	2.4	2.4 b	1.4 b	11.0	10	3.3	7.4	2.2
BARD 1–3 1999										
AM	2.3 a	17.4 a	3.1	2.3	1.2	13.8 a	7.8	6.7	10.2	2.1
GM	2.7 b	14.6 b	3.5	2.2	1.1	12.0 b	7.5	5.2	8.7	2.1

[a] Means followed by different letters within a study and column are significantly different according to ANOVA, $P<0.05$

Table 2 Means for nine phenotypic traits of androgenic (AM) and gynogenic monoploids (GM) derived from the *S. phureja* families PP5 and BARD 1–3 in field studies conducted over 2 years

Monoploid type	Vigor	Height	Shoot no	Leaf length	Leaf width	Leaflet no	Tuber no	Tuber wt	ATW
PP5 1998									
AM		26.6	3.3 a[a]	9.5 a	5.8 a	12.8	6.7 a	29.7 a	4.4
GM		26.3	2.0 b	8.2 b	4.9 b	12.4	1.8 b	11.3 b	6.3
PP5 1999									
AM	4.2	13.1 b	2.8				1.2	11.8 a	9.8
GM	4.1	16.6 a	1.9				0.8	3.4 b	4.25
BARD 1–3 1999									
AM	3.7	11.1	5.6 a				4.5	9.2	2
GM	3.9	10	1.7 b				1.9	2.1	1.1

[a] Means followed by different letters within a study and column are significantly different according to ANOVA, $P<0.05$

ternode length and leaf length, indicating the presence of position effects in the greenhouse.

A total of 395 pollinations was performed on androgenic and gynogenic PP5 monoploids. However, only three androgenic clones set fruit. One was later found to be diploid, probably due to spontaneous chromosome doubling. Crosses between PP5–53 and ID5 yielded three fruits, but the plants died prematurely, resulting in underdeveloped fruits without seeds. A third androgenic clone, PP5–3S-21, re-confirmed as monoploid from a greenhouse leaf sample, set four fruits containing 6–15 seeds each.

Greenhouse experiment 2

For the ten traits examined, five exhibited significant differences between derivations, either in one family or the other (Table 1). All the significant differences indicated greater vigor of androgenic over gynogenic populations. In the *S. phureja* PP5 family, the average terminal leaf length and leaf width were significantly larger by 13 and 14%, respectively, in the androgenic monoploids (2.7 vs 2.4 cm for length; 1.6 vs 1.4 cm for width). Vigor, plant height, and average leaflet number were significantly greater in the BARD 1–3 androgenic monoploids than in the BARD 1–3 gynogenic monoploids [2.3 vs 2.7 vigor rating (17%), 17.4 vs 14.6 cm height (19%), and 13.8 vs 12.0 leaflets (15%), respectively, for androgenic and gynogenic monoploids]. In a combined analysis of data (not shown) from both families, leaf length and leaflet number were significantly greater in the androgenic populations.

Field studies

In the 1998 field study of PP5 monoploids, five of the eight traits observed revealed significant differences for derivation, all indicating a better performance of androgenic vs gynogenic plants (Table 2). Androgenic plants had 65% more shoots (3.3 vs 2.0), larger leaves [9.5 vs 8.2 cm leaf length (16% longer) and 5.8 vs 4.9 cm leaf width (18% wider)] and better tuberization [6.7 vs 1.8 tubers per plant (272% more) and 30 vs 11 g tubers per plant (163% greater)]. A sample of monoploid tubers harvested from the field is shown in Fig. 1.

In 1999, the study was repeated with a total of 49 monoploids from both the PP5 and BARD 1–3 families. Significant differences for derivation varied with the

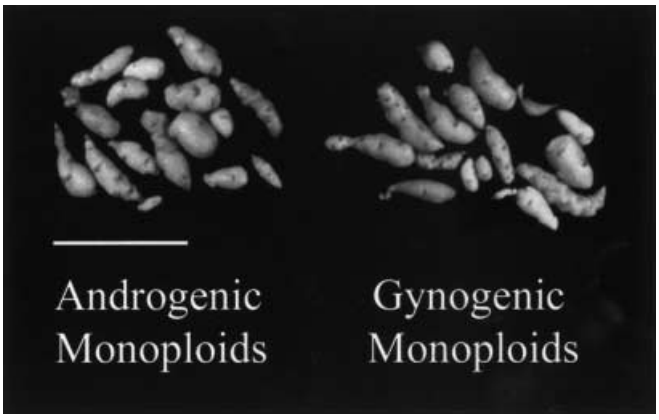

Fig. 1 Tubers harvested from field-grown plants of various androgenic and gynogenic monoploids derived from *S. phureja* clone PP5 (bar=10 cm)

Table 3 Mean frequency of 1*x*, 2*x* and 4*x* cells in androgenic and gynogenic BARD 1–3 monoploids

Type	Frequency of cells at ploidy		
	1*x*	2*x*	4*x*
Androgenic	41% b[a]	45%	14% a
Gynogenic	43% a	46%	11% b

[a] Means followed by different letters within columns are significantly different according to ANOVA, $P<0.05$

family (Table 2). For the PP5 family, plant height was significantly greater (27%) for the gynogenic plants (16.6 vs 13.1 cm), whereas total tuber yield was four times greater for the androgenic plants (12 vs 3 g). For the BARD 1–3 family, shoot number was the only significant difference due to derivation [5.6 for androgenic plants and 1.7 for gynogenic plants (229% more shoots)]. Four of the six traits were significantly different in a combined analysis (data not shown). Only plant height was greater in the gynogenic population, which may have been due to significantly fewer stems. All of the other significant differences in the field studies indicated a better performance of androgenic plants.

DNA comparison

One plant was found to be diploid after flow cytometry and was discarded, resulting in a total of 39 BARD 1–3 monoploid plants analyzed (19 androgenic and 20 gynogenic). In a combined analysis of the two experiments, ANOVA revealed significant differences in peak positive values for 1*x* and 4*x* peaks due to the experiment and the monoploid clone, but not for derivation (Table 3). The percent cells at the 1*x* and 4*x* levels was significantly different between derivations and among plants, with 5% fewer monoploid cells and 27% more tetraploid cells for the androgenic population (Table 3).

Discussion

In 17 of 51 comparisons, including both greenhouse and field studies, between androgenic and gynogenic monoploids of two selections from different accessions of *S. phureja*, the androgenic monoploids were significantly more vigorous in several measures of growth than the gynogenic monoploids. Only two significant differences appeared to favor the gynogenic monoploids (plant height). The greater height of the gynogenic monoploids may have been due to decreased stem number. The superior performance of the androgenic monoploids relative to the gynogenic was an unexpected result. In almost all comparisons of haploid derivation mechanisms in other crops, gynogenic performance equalled or exceeded androgenic performance. This is the first such comparison of monoploid derivation mechanisms in a highly heterozygous cross-pollinating species expected to bear lethal and deleterious genes.

Possible reasons for the differences between the androgenic and gynogenic populations are differential selection pressures, incorporation of genes from the haploid-inducing pollinator in the gynogenic monoploids, and genomic changes inherent in either haploid-derivation process, such as increased DNA content per cell (De Paepe et al. 1981) or other manifestations of gametoclonal variation (Veilleux 1998). One obvious difference between the two populations of gametes from which candidate monoploid genotypes are derived is size. Anther-derived plants originate from a much greater number of potentially embryogenic microspores compared with gynogenic plants originating from considerably fewer fertilized ovules. The early events of embryogenesis are under the direction of the diploid genome of the sporophyte and are nurtured by the endosperm during gynogenesis. In contrast, the haploid genome of an anther-derived embryo must function exclusively, utilizing nutrient medium, during androgenesis, resulting in greater selection pressure.

We did not expect fruit set to result from pollinating the monoploids with pollen from a diploid clone. These fruits could have resulted either from normal reproduction on spontaneously occurring diploid sectors of the monoploid or from unreduced female gamete formation in the monoploid. PP5 is known to produce a variable frequency (>1% to <5%) of 2n male gametes by the fusion of second-division spindles, a mechanism similar to first-division restitution (Veilleux et al. 1985). If the putative monoploid clones PP5–53 and PP5–3S-21 had not spontaneously doubled, seed set in monoploids would indicate that they produced viable unreduced (1n=1*x*=12) female gametes. Unreduced female gametes have been reported to occur in diploid potato germplasm by two mechanisms that are genetically equivalent to first-division restitution (FDR). These two FDR mechanisms, delayed meiotic division and synaptic mutation, could give rise to viable unreduced female gametes in monoploid potato. In a survey of five diploid potato species, 24% of 127 plants were found to produce viable 2n eggs at a fre-

quency of 5–57% (Werner and Peloquin 1991). Although three SDR-type mechanisms of 2n egg formation have also been reported in potato (Werner and Peloquin 1991), they require a normal first meiotic division and, therefore, would be precluded in monoploids.

We utilized flow cytometry to detect variation for DNA content and a propensity toward endopolyploidization between the androgenic and gynogenic populations. If androgenic potato monoploids behaved similarly to anther-derived tobacco dihaploids (Dhillon et al. 1983), then increased DNA content would have been expected in the androgenic monoploids. However, no such trend was found for potato. Although considerable differences in DNA content for the peak positive values were observed among monoploids, there was no difference between derivations. A significant difference for peak positive values between experiments may be explained by an inconsistency in experimental protocol, such as increased staining time before flow cytometric analysis in one experiment or drift in settings of the flow cytometer. Replication effects were significant for peak positive values in both experiments, emphasizing the need for replication in flow studies, lest artifactual differences in perceived DNA content be attributed erroneously to genotype.

That a significantly greater frequency of cells in the androgenic plants was tetraploid suggests a higher rate of endopolyploidization of androgenic compared to gynogenic plants. A higher frequency of polyploid cells that have generally larger dimensions could have caused enlargement of organs in the androgenic plants, underlying some of the morphological differences observed between derivations in the greenhouse and field studies.

Anther culture is generally considered a more efficient means to produce monoploids than gynogenic mechanisms in potato; however, both processes are affected by parental genotype. Efficiency of the derivational processes is primarily controlled by the anther donor or seed-parent genotype, but the haploid-inducing pollinator also affects the efficiency of gynogenesis (Hermsen and Verdenius 1973). Since the responses appear uncorrelated, it is likely that different genes control them so that one mechanism may be much more efficient for a given clone.

Working with monoploids derived from a heterozygous cross-pollinating species presents certain obstacles to experimental manipulations. Depending upon the level of inbreeding depression incurred during the haploidization of selected parental clones, the monoploids will exhibit more or less vigor. Uijtewaal et al (1987) and van Breukelen (1981) have described monoploids of *S. tuberosum* derived after two cycles of gynogenesis, first from tetraploid cultivars and subsequently from dihaploids selected for sufficient fertility to permit fruit and seed set. These monoploids were insufficiently vigorous to allow field experiments comparable to the ones we conducted in the present study. Although our *S. phureja* monoploids were more vigorous, our efforts were still frustrated by losses at every stage of propagation, i.e., acclimatization of in vitro plantlets, vegetative propagation of greenhouse plants by cuttings, emergence of plants from greenhouse-grown tubers, and survival in the field. Hence, we needed to consider alternative experimental designs for field plots in order to accommodate as many genotypes as possible for the comparison of derivations. Despite such differences in design, all of the experiments were in remarkable agreement.

It is evident from this study that the array of genotypes produced via androgenesis was consistently superior to the array of genotypes produced gynogenically. The heightened performance of the androgenic monoploids could be due to agronomically useful selection within androgenesis, a negatively impacting selection within gynogenesis, or a combination of both factors in potato. If other cross-pollinated species are affected similarly by the derivation mechanism, then anther culture could be used preferentially if either method is feasible. Molecular analyses may shed light on the origin of the selection pressures at work.

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