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BREEDING POTENTIAL OF GROUP ANDIGENA HAPLOID POTATOES

A thesis submitted to the Graduate School of the
University of Wisconsin-Madison in partial fulfillment of
the requirements for the degree of Doctor of Philosophy

BY
JUAN A. ^{LEJANDEO} LANDEO

Degree to be awarded: December 19____ May 19____ August 19 79

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BREEDING POTENTIAL OF GROUP ANDIGENA HAPLOID POTATOES

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A thesis submitted in partial fulfillment of the
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DOCTOR OF PHILOSOPHY
(Plant Breeding and Plant Genetics)

UNIVERSITY OF WISCONSIN - MADISON

1979

ABSTRACT

BREEDING POTENTIAL OF GROUP ANDIGENA HAPLOID POTATOES

Juan A. Landeo^{LEJANDRO}

Under the supervision of Professor R. E. Hanneman, Jr.

The great genetic diversity present in Solanum tuberosum Gp. Andigena ($2n = 4x = 48$), justifies the exploitation of such germplasm in potato improvement, whether using the traditional breeding scheme at the tetraploid level or the $2n$ gamete approach.

The $2n$ gamete breeding scheme, proposed by Chase (1963) and amended by Mendiburu, Peloquin and Mok (1974), is considered, theoretically, to be the most efficient method by which yield improvement in potato can be made. Suitable F_1 hybrids among diploid sources are crossed in the first step of the scheme to synthesize a tetraploid genotype, through the occurrence of $2n$ gametes, particularly those from first division restitution (FDR).

Haploids from Gp. Andigena would be one way to explore the genetic reservoir present in this Group, and the $2n$ -gamete approach, the best scheme in which they could be used. Their diversity and cultivated nature would satisfy some of the requirements of the $2n$ -gamete breeding scheme in maximizing heterosis.

The breeding potential of Gp. Andigena haploids has been investigated in the present study through the use of a wide sample of haploids from the original parental introductions.

The crossing behavior of Group Andigena haploids (AH), with Gp. Tuberosum haploids (TH), Gp. Phureja (PHU), and Gp. Stenotomum (STN)

was excellent. Male and female fertility of AH was relatively high, as judged by seed per fruit in crosses to PHU, STN and TH, particularly when PHU and STN served as one of the parental sources.

A Group diallel cross was used to investigate the heterosis and combining ability of AH with TH, STN and PHU, using six quantitative traits - total tuber weight, fresh vine weight, tuber + vine weight, dry vine weight, total dry matter weight (tuber + vine), and specific gravity - at two locations.

The AH F_1 hybrids with TH, PHU and STN did not express heterosis for total tuber yield on a Group-population basis. The lack of adaptation of AH for tuberization under long daylengths was presumed to be mainly responsible; however heterosis was expressed for dry vine weight and total dry matter weight as 5% and 5.9% over the midparental values, respectively. Hybrids among TH, STN and PHU did show heterosis for total tuber yield.

Combining ability analyses among these four Groups - AH, TH, STN, PHU - demonstrated significant general combining ability for total tuber yield and specific gravity. Additive genetic effects were mainly important in these populations, and the narrow sense heritability values were relatively high for a quantitative trait. Specific combining ability was not significant for any of the six traits.

Genetic variation was studied on a sample of AH clones for the same six traits considered in the diallel design. Design I and the Parent-offspring regression were used to estimate genetic variances. The amount of additive genetic variance (σ_A^2) was higher than dominant

genetic variance (σ_D^2) for total tuber weight. The remaining traits had both σ_A^2 and σ_D^2 being equally important. The amount of total genetic variance, as judged by the genetic coefficient of variation (GCV), was high. These GCV's ranged from 25 percent to 93 percent among all traits. Narrow sense heritability values obtained by both methods - Design I and P.O. regression - were relatively high for all quantitative traits, and slight discrepancies between the two analyses were observed.

Both the Diallel design on a Group population basis and Design I and Parent-offspring regression on a sample of AH clones, indicated a sufficient amount of additive genetic variance on which progress from selection would be made if these populations were to undergo selection.

The frequency of 2n gametes in the hybrid populations from the diallel cross, was estimated by the amount of seed set. For 2n pollen, 4x x 2x crosses were used and the percentage of large stainable pollen was also considered; and for 2n eggs, 2x x 4x crosses were used. In both instances, the amount of seed set was not high; but variation did exist depending on the tetraploid parent used, suggesting that both diplandrous and diplogynous clones with high frequency of 2n gametes could be identified. Male and female fertility in the Group-hybrid families were found to be reasonably high for AH x PHU, AH x STN and their reciprocals; TH x AH, TH x STN and TH x PHU were highly male sterile but female fertile.

The results of the evaluation of the breeding potential of Gp. Andigena haploids in the present study, will aid in the basic

understanding of their use, and in the effective use of their parental germplasm in the 2n gamate breeding approach to potato improvement.

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GENERAL INTRODUCTION

One of the two main avenues of potato breeding for improvement of tuber yield and related commercial quantitative traits, has been and still is carried on at the tetraploid level, which is the level of all the highly productive commercial cultivars. Two tetraploid cultivated taxonomic Groups are distinguished among the tuber-bearing Solanum species; Solanum tuberosum Group Tuberosum and Group Andigena ($2n = 4x = 48$). The former Group is mainly cultivated in the north temperate latitudes with long daylengths (15-17 hr). It has been speculated that this Group evolved through adaptation for tuberization under long days from a few Gp. Andigena introductions to Europe in late 16th century (Howard, 1970; Salaman and Hawkes, 1949; Simmonds, 1969). The nature of the genetic base of Gp. Tuberosum has been postulated as already being narrow by the time modern potato breeding was started (Horsfall, 1972; Howard, 1970; Simmonds, 1969). Mendoza and Haynes (1973), from a coancestry analysis study of a group of North American cultivars, indicated that the genetic relationship among the present cultivated varieties was closer than had been postulated. He pointed out that the genetic uniformity of the present cultivars might present a potential for epidemics, and make difficult further significant improvement. The second Group, (Gp. Andigena), grows at lower latitudes and shorter daylengths (11-13 hr). This last Group is widespread along the Andean mountain ranges from northern Colombia down to north-west Argentina. Its diversity is immense and it constitutes a huge genetic reservoir in which most desirable traits can be found and utilized.

Early attempts at hybridization between these two Groups were discouraging due to the transmission of poor tuberization and lateness to the hybrids from Gp. Andigena (Simmonds, 1960). Simmonds (1960), designed a long-term experiment to recreate Gp. Tuberosum; consequently, providing a new genetic base for potato improvement. Paxman (1965), using selected clones from Simmonds's partially improved Gp. Andigena populations - later named Neo-tuberosum, determined heterosis upon crossing to Gp. Tuberosum cultivars. After additional cycles of selection for tuberization in Neo-tuberosum; heterosis was demonstrated independently again for tuber yield by the hybrid families from selected clones of Neo-tuberosum and Gp. Tuberosum cultivars (Cubillos and Plaisted, 1976; Glendinning, 1969; Tarn and Tai, 1977). The apparent difficulty in potato improvement of Gp. Tuberosum at the tetraploid level, appears to have been overcome so far as tuber yield is concerned, by the addition and the use of the new adapted tetraploid genetic source - Neo-tuberosum.

A second method of potato improvement, which is not widespread yet, was developed as a result of haploid extraction and the possible uses of haploids in potato breeding as suggested by Hougas and Peloquin (1958). Gene transfer from diploid species to tetraploid cultivars through hybridization with their haploids, and the occurrence of "unreduced gametes" ($2n$) of the haploid-species hybrid sources were the main considerations. As a consequence of haploid extraction from tetraploid cultivars; the efficiency of extraction following interploidy matings, crossability with diploid species, vigor, fertility, microsporgenesis,

etc. were extensively studied mainly in Gp. Tuberosum (Hougas et al, 1958; Hougas et al, 1964; Montelongo-Escobedo and Rowe, 1969; Peloquin and Hougas, 1958, 1959, 1960; Peloquin et al, 1966; Perez-Ugalde et al, 1964; Ross et al, 1964; Yeh et al, 1964). De la Puente (1973), studied the frequency of haploid extraction in Gp. Andigena cultivars. He also examined the fertility and crossability of two selected Gp. Andigena haploids. Hanneman and Ruhde (1978), also examined the frequency of haploid extraction in 66 different Gp. Andigena introductions.

The ease of haploid extraction, and the feasibility of haploid-diploid species hybridization, led Chase (1963), to outline a hypothetical analytical breeding scheme in Solanum tuberosum utilizing haploids and other diploid stocks. In essence, what the scheme proposed was, a) the reduction of the autotetraploid to the diploid level by parthenogenesis, b) intensive breeding and selection at the diploid level to achieve desired genetic combinations, and c) resynthesis of the tetraploid by doubling the desired genotype obtained. In his alternate scheme, Chase suggested that the desired 24-chromosome breeding stocks be intercrossed directly in an effort to take advantage of the functioning of "unreduced gametes" to synthesize the tetraploids directly.

The occurrence of 2n gametes in the tuber-bearing Solanums, was reported or implied in earlier studies as a result of inter-ploidy crosses (4x x 2x) (Ivanoskaja, 1941; Koopmans and Van der Burg, 1952; Oppenheimer, 1933). Swaminathan and Howard (1953), in both 4x x 2x and 2x x 4x matings, also obtained predominantly tetraploid progeny inferring the occurrence of 2n gametes.

Harlan and de Wet (1975), discussing the dynamics of $2n$ gametes in polyploid evolution, listed 85 genera comprising several hundred species, in which chromosomal increase occurs through the union of gametes one or both of which are $2n$. They divided the occurrence of $2n$ gametes in two classes: Class I, where chromosome increase through $2n$ gametes, occurs in the first generation in selfed progenies, sibs within inbreds and among interbreeding populations as well as crosses between ecotypes, species and/or genera, and Class II in which chromosome increase occurs in the offspring of a hybrid with meiotic disturbances that result in $2n$ gametes. This event may occur in F_2 or BC_1 progeny or on crossing the F_1 to a third parent, but occurs in the second generation in contrast to that of Class I. Examples in Class I, perhaps are best known in the genera: Agropyron, Apium, Beta, Botriochloa, Brassica, Caltha, Citrus, Crepis, Cynodon, Dianthus, Dichanthium, Fragaria, Lycopersicon, Medicago, Musa, Oenothera, Oryza, Petunia, Poa, Potentilla, Primula, Prunus, Rubus, Saccharum, Solanum and Triticum. In Class II, a few classic cases would be represented in the offspring of the following crosses: Nicotiana rustica x Nicotiana paniculata, Digitalis purpurea x Digitalis ambigua, Raphanus x Brassica, Triticum crassum x Triticum turgidum, Triticum vulgare x Agropyron intermedium, Oryza sativa x Oryza officinalis, Arachis villosa x Arachis hypogaea, etc.

It is evident that Class I events can also induce Class II polyploids. For instance a spontaneous triploid originated by the fusion of $2n$ and n gametes can eventually produce hexaploids in the F_2 generation by the functioning of $2n$ gametes in both sexes; or tetraploids if it is backcrossed to a normal diploid by $2n$ and n matings. The occurrence of

2n gametes in plant species, as indicated by Harlan and de Wet, and their function in polyploidy is not a rare event.

Hanneman and Peloquin (1967), studying the feasibility and effectiveness of obtaining tetraploid potatoes from direct crosses between 24-chromosome haploid-diploid hybrids and 48-chromosome cultivars, obtained primarily tetraploid progenies from $4x \times 2x$ and $2x \times 4x$ crosses. They pointed out that the simplicity and efficiency of this breeding technique would warrant its use in germplasm transfer from the diploid to the tetraploid level.

High yielding tetraploids were obtained from $4x \times 2x$ and $2x \times 4x$ matings including certain Gp. Phureja-Tuberosum haploid hybrids, previously selected by Hanneman and Peloquin (1967, 1968), and tetraploid cultivars (De Jong and Tai, 1977; Kidane-Mariam, 1975; Mendiburu, 1971; Mok and Peloquin, 1975; Quin and Peloquin, 1973). Heterosis of the resulting tetraploid families following $4x \times 2x$ crosses was explained, cytologically and genetically, on the basis of the nature of 2n pollen formation by first division meiotic restitution (FDR) due to parallel spindles (Mendiburu, 1971; Mok and Peloquin, 1974; Mok and Peloquin, 1975; Wang, Peloquin and Meniburu, 1971). The value of 2n pollen (diplandroids) formed by FDR is to provide a unique method for transferring beneficial intra- and inter-locus interactions from an already heterotic genotype to the offspring.

A unique potato breeding method, analogous to Chase's alternative scheme (1963), designed to capitalize on disomic inheritance, genetic diversity and bilateral sexual polyploidization, was proposed by

Mendiburu, Peloquin and Mok (1974). In this scheme, FDR is assumed to operate in $2n$ -gamete formation of at least one sex. The tetraploid nature of the final product, its asexual mode of reproduction and FDR $2n$ gametes would provide a unique opportunity to accumulate and compound additive and non-additive genetic effects at higher ploidy levels, and also result in the immediate fixation of these effects. Two levels of heterosis are discussed to occur by these authors, one occurring in the two single cross hybrids at the diploid level and a second level of interactions in the final cross depending not only on FDR but also on the degree of relatedness or divergency between the two diploid hybrids.

The superiority of the tetraploids obtained by unilateral or bilateral sexual polyploidization as a function of FDR $2n$ gametes, undoubtedly has added a new dimension to potato breeding as well as to genetic, cytogenetic and evolutionary studies.

It is the second method of potato improvement suggested by Mendiburu, Peloquin and Mok (1974), that the present research is concerned with. The results of an extensive study of *Gp. Andigena* haploids will be presented in following sections. Upon examining the intensive breeding at the diploid level as a part of this second method of potato improvement, immediately questions arise related to heterosis, genetic variation, nature of gene action, heritabilities, etc. in the material under study. Since it is believed that there is much genetic diversity among the cultivated species, the use of these cultivated sources in this method would be desirable. Maximum heterozygosity can

be obtained upon crossing these Groups, and heterosis expressed, since they are sufficiently divergent. It is the author's opinion that the cultivated germplasm comprised by the two tetraploid Groups and the diploid Groups, should be of first-choice in potato improvement due to the large genetic diversity that they have. Besides, their cultivated nature would facilitate greatly their use in breeding. The wild species should be brought into the cultivated forms as needed, particularly whenever desirable traits are not found among cultivated sources.

Diploid cultivated potatoes including haploids from tetraploid sources, are enforced open-pollinators due to the self-incompatibility mechanism that they possess (Cipar, 1963; Cipar et al, 1964; Hawkes, 1958; Pushkarnath, 1942; Smiley, 1963); consequently, they are highly heterozygous or can be in the case of haploids upon crossing. If we think of each Group within S. tuberosum, as being composed of highly heterozygous individuals, a sample of them would represent a particular Group population equivalent to that of an open-pollinated variety of corn; and if these Groups are handled as populations, they will preserve a wide range of genetic variability that can be maintained and improved.

Heterosis of population crosses of various species have raised increased interest in recent years, in providing a basis for more efficient breeding procedures in both plants and animals (Lonnquist and Gardner, 1961; Robinson et al, 1955; Wallace, 1955). Robinson et al (1955), using a diallel design in corn varieties, reported heterosis values of the F_1 's as high as 19.9% over the mid-parent and 11.5% more than the highest parent. Likewise, Lonnquist and Gardner (1961), using

a different stock of open-pollinated corn varieties in a diallel cross, reported heterosis values of from 4.0 to 8.5%.

The use of Group crosses in potato as done for open-pollinated corn varieties, would help in the selection of suitable stocks on which a selection program could be started whether single or hybrid populations were to be worked with. The upgrading of these diploid populations for desirable traits will eventually provide selected clones to reconstitute tetraploid genotypes through bilateral sexual polyploidization.

The availability of Gp. Andigena haploids and our interest to promote their use, also prompted us to assess their genetic variation. Genetic designs such as Design I, described by Comstock and Robinson (1948), and used in diploid potatoes by Rowe (1969), were used to quantify the genetic variation of a sample of clones within Gp. Andigena haploids.

The certainty of the frequency of $2n$ gametes in the diploid Group-hybrid populations, would warrant the synthesis of the desired tetraploid genotypes.

The objectives of the present study were as follows: (1) To determine the crossability of Gp. Andigena haploids; (2) To estimate heterosis and gene effects of Gp. Andigena haploids in a diallel cross with Gps. Phureja, Stenotomum and Tuberosum haploids; (3) To determine genetic variation in Gp. Andigena haploids; and (4) To estimate fertility and $2n$ -gamete frequency in hybrid families from crosses among Gp. Andigena haploid, Gp. Tuberosum haploid, Gp. Phureja and Gp. Stenotomum.

Crossability of Solanum tuberosum Gp. Andigena Haploids

INTRODUCTION

The possibility of using haploids from Solanum tuberosum L. for cytogenetic and genetic studies as well as breeding was first proposed by Hougas and Peloquin (1958). Since then many haploids have been obtained and utilized. The disomic inheritance and direct approach to gene transfer from wild and cultivated diploid related species make haploids unique for study.

Hougas and Peloquin (1960) studied the crossability of Gp. Tuberosum haploids with certain of the diploid Solanum species. Most of these haploids were only used as the pistillate parent, because their female fertility was relatively high, whereas the pollen fertility of many haploids was low (Peloquin and Hougas, 1960). Only two haploids, US-W1 and US-W4, were found to be male fertile and used as both male and female parents. Their results indicated that haploids cross well with other diploid related species and most haploid-diploid species hybrids were reported to be vigorous plants.

Ross, Peloquin and Hougas (1963), studied male and female fertility among 60 F_1 's of Gp. Phureja and Gp. Tuberosum haploid crosses. These F_1 's represented 15 Gp. Phureja introductions, used as females and two male-fertile haploids (US-W1 and US-W42) used as males. All 60 hybrid selections proved to be highly male and female fertile as judged by the seed set per fruit obtained upon inter-crosses among them.

Perez-Ugalde, Hougas and Peloquin (1964), also studied fertility in the F_2 generation of Gp. Phureja and Gp. Tuberosum haploid hybrids.

Tests for female fertility were based on fruit per pollination and seed per fruit, and male fertility was evaluated on the basis of pollen shedding, pollen germination in vitro and seed set per fruit. Sixty three percent of the clones tested were female fertile and 77 percent were male fertile. Only two haploids, US-W1 and US-W42, served as males in this study.

Other studies of the crossability of Gp. Tuberosum haploids as well as their hybrids with Gp. Phureja were reported elsewhere (Bender, 1963; De la Puente, 1973; Sosa-Chavez and Hernandez de Sosa, 1972); however, few or none involved Gp. Andigena haploids.

The present study, was conducted to estimate the general crossing behavior of Gp. Andigena haploids with Gps. Phureja, Stenotomum, and Tuberosum haploids as a part of a larger study to explore the breeding potential of Gp. Andigena haploids.

MATERIALS AND METHODS

Two hundred haploids from Solanum tuberosum Group Andigena involving 59 Gp. Andigena introductions were derived from previous inter-matings between a random sample of Gp. Andigena clones and one selection of Gp. Phureja P.I. 225682 (1.22), which is known to be a good haploid inducer. They were propagated by stem-cuttings to increase the number of plants per haploid to ten. In early June at Sturgeon Bay, four plants of each haploid were transplanted to 6-inch pots in the screenhouse, and the remaining six plants were transplanted to the field. Selected bulk populations of Gp. Phureja (200 clones) and Gp. Stenotomum (189 clones) and haploid clones of Gp. Tuberosum were planted as source materials for crossing with Gp. Andigena haploids.

Crosses were initiated in early July and ended the first week of September. The cut-stem technique was used for plants grown in the field, and stems were placed in milk bottles in an air-conditioned glasshouse at 21-26°C. The open flowers were removed and the remaining large closed buds (4-5 per stem) were emasculated. Pollination followed the same day or the next morning. On-plant pollinations were done in the screenhouse the day after bud emasculation.

The pollen source for each group came from bulking an equal number of flowers per clone - two to three flowers for Groups Phureja and Stenotomum and more than 10 for Groups Tuberosum and Andigena haploids. The extracted pollen was used the same day or stored in a refrigerator (4°C) and used for no more than one week. Gelatin capsules filled with bulk pollen were used to pollinate emasculated

flowers by dipping the stigmas into the capsule. After 10 days stems without fruits were discarded and those with fruit were held for another 4-5 weeks, at which time fruits were harvested. A minimum of four weeks after fruit harvesting, seed extraction was begun.

The mating scheme followed was designed to test crossability of Gp. Andigena haploids (AH), with Groups Phureja (PHU), Stenotomum (STN), and Tuberosum haploids (TH). Reciprocal crosses were made to determine the female and male fertility of the AH group.

To check for possible factors affecting seed set, four styles per clone from a sample of Gp. Andigena haploids were pollinated with Gp. Andigena haploid bulk pollen and with Gp. Phureja bulk pollen. Forty-eight hours after pollination styles were collected and fixed in FAA (1:1:8, formalin-aceto-alcohol) solution. The styles were placed in 8N NaOH for 8-24 hours to soften the tissue and then transferred to 0.1% aniline blue dye in 0.1N K_3PO_4 (4-8 hr.) for staining. After staining, they were removed, mounted on slides and observed under ultra-violet microscopy (Martin, 1958). Pollen tube growth was scored according to where a majority of the pollen tubes stopped in the style: upper, middle or lower third.

RESULTS

Crossability.

A total of 14,530 pollinations were made on 693 clones of which 408 set fruit. Approximately 43% of the pollinations were successful (Table 1).

With AH as the female, percentages of AH clones that set fruit were 43 when crossed with AH bulk pollen, 17 with TH bulk pollen, and 66 and 62 with bulk pollen of PHU and STN, respectively. With AH pollen on PHU, STN and TH, the percentages of clones that set fruit were 93, 55 and 62, respectively. In contrast, with TH clones as the female the percentages of clones that set fruit with bulk pollen of TH, PHU, STN and AH were 37, 73, 70 and 62, respectively.

Among clones that successfully set fruit, the crossability pattern (Table 2), appears as follows: AH clones crossed as females with PHU, STN, and TH yielded an average of 47.7, 38.3 and 6.2 seeds per fruit, respectively. The average female fertility of AH was relatively high with good pollen (PHU and STN), but this was not true for TH which apparently had low pollen fertility. In contrast, the female fertility of TH tested with PHU and STN was acceptable (22.3, 19.5 seeds/fruit, respectively), but less than that of AH.

Bulk pollen from AH, on AH, PHU, STN, and TH clones gave averages of 24.7, 69.0, 43.3, and 20.8 seeds/fruit, respectively. These values indicated that the male fertility of AH was satisfactory, even when crossed onto its own group which might have some self-incompatible alleles in common. Seed set was reasonably high, but not as high as with PHU or STN.

Table 1. Effectiveness of Gp. Andigena haploids as a male and female parent when crossing with Gp. Tuberosum haploids, Gp. Phureja and Gp. Stenotomum.

Crosses	Total Clones	No. Clones Setting Fruit	Percent Clones Setting Fruit	Total Pollinations	Successful Pollinations	Percent of Successful Pollinations
AH x PHU	79	52	65.8	1,883	820	43.5
AH x STN	71	44	62.0	1,651	721	43.6
AH x TH	40	7	17.5	1,248	136	10.9
AH x AH	90	39	43.3	3,962	1,123	28.3
PHU x AH	71	66	93.0	1,231	962	78.1
STN x AH	53	29	54.7	726	347	47.8
TH x AH	74	46	62.2	1,054	645	61.2
TH x PHU	64	47	73.4	844	634	75.1
TH x STN	69	48	69.6	824	534	64.8
TH x TH	82	30	36.6	1,107	362	32.7
Totals	693	408	58.9	14,530	6,284	43.2

AH = Gp. Andigena haploid
 TH = Gp. Tuberosum haploid
 STN = Gp. Stenotomum
 PHU = Gp. Phureja

Table 2. Comparison of the crossability of S. tuberosum Gp. Andigena haploids with Gp. Tuberosum haploids, Gp. Phureja, and Gp. Stenotomum.

Crosses	No. Female Clones	No. Pollinations	No. Fruits	No. Seeds	Seeds/ Fruit	Range of Seeds/Fruit
AH x PHU	52	820	412	19,638	47.7	0.8 - 156
AH x STN	44	721	302	11,575	38.3	0.6 - 140
AH x TH	7	136	32	198	6.2	0.5 - 20
AH x AH	39	1,123	331	8,175	24.7	1.0 - 60
PHU x AH	66	962	456	31,467	69.0	21.7 - 150
STN x AH	29	347	125	5,410	43.3	6.6 - 100
TH x AH	46	645	238	4,951	20.8	0.5 - 75
TH x PHU	47	634	260	5,802	22.3	0.5 - 74
TH x STN	48	534	335	6,541	19.5	0.2 - 85
TH x TH	30	362	110	779	7.1	0.2 - 75

Finally, when comparing only AH and TH, AH as a male crossed onto itself and TH resulted in 24.7 and 20.8 seeds/fruit, respectively, Whereas, TH as a male crossed with itself and AH gave 7.1 and 6.2 seeds/fruit, respectively.

When crossability behavior was compared between AH and TH as females with PHU and STN as males, AH showed more seeds/fruit, and twice the range of seed/fruit indicating superior variability for female fertility in AH (Table 2). Similarly, AH as a male on PHU and STN gave a wide range of seed set, reaching upper limits of 150 and 100 seeds/fruit, respectively. Since TH is known to be highly male sterile (Peloquin and Hougas, 1958; Ross, Peloquin and Hougas, 1964), it was not crossed to PHU or STN.

Pollen Tube Growth.

Table 3 summarizes pollen tube data. Sixty-six AH clones were crossed with their own bulk pollen and 55 with bulk pollen from PHU. The average number of pollen tubes in the stigma portion compared to the lower portion of the style for AH x AH was in the range of 31-50 to 1-15, respectively, and over 500 to 101-500, respectively, for AH x PHU. Pollen tubes in the middle third of the style, although recorded, were not included in the table. The range of variability among clones was extremely great for AH x AH and consistent for AH x PHU.

Table 3. A comparison of pollen tube growth in the upper and lower third of the style in AH x AH and AH x PHU crosses.

Crosses	No. Female Clones	Pollen Tube Growth				Most Frequent Class Ratio
		Average* Stigma/Bottom Ratio	Range of Stigma/Bottom Ratio			
AH x AH	66	3:1	1:0 - 5:5		variable	
AH x PHU	55	6:5	4:3 - 6:6		6:6	
* 0	0 pollen tubes	3	31-50 pollen tubes	6	> 500 pollen tubes	
1	1-15 "	4	51-100			
2	16-30 "	5	101-500			

DISCUSSION

As in previous studies on crossability, the natural environment was noted to have a significant effect on the successfulness of crossing. The percent of successful pollinations ranged from 11 to 75 (Table 1), and the overall percent of clones setting fruits was 58.9 which represents only 43.2 percent of the total pollinations. Undoubtedly the high temperatures during early and mid-summer prevented the success of about half of the pollinations. This agrees with a previous report (Hollenback, 1966) that high temperatures interacting with different relative humidities caused reduced pollen viability, and reduced fruit and seed set. Early dropping of young buds, flower abscission, lack of flowering, and profuse flowering without fruit set after pollination were frequently observed in the material used in this study. These characteristics might also be partially associated with environmental effects as well as with female sterility especially in AH and TH (Perez, Hougas and Peloquin, 1964).

The relatively high female and male fertility within AH has been clearly indicated in this study, and may be explained by the high heterozygosity that is inherent in the parental Group Andigena clones associated with the wide geographic distribution of the parental introductions utilized. The great diversity in Gp. Andigena can be speculated to provide enhanced heterozygosity as a result of intercrossing; thus allowing more opportunity for the allelic constitution of most loci to diversify. Introgression of diploid relatives, having screened-out most deleterious recessive alleles more efficiently, into

tetraploids would have lead to less exposure of such alleles among haploids isolated from them. It is not unusual to see volunteers coming from true seeds among native farmer's fields in the highlands in the South American Andes; therefore if these volunteers have any selective value, they would be kept by the farmers and thus enter the pool of Gp. Andigena native cultivars. Another way heterozygosity could have been increased would be through the occurrency of $2n$ gametes, particularly those arising from first division restitution (FDR). Ploidy mixtures of cultivated varieties are not uncommon in native farmer's fields in the highlands. The introgression of already heterozygous diploids through FDR $2n$ gametes to tetraploid cultivars, may have added heterozygosity and improved the allelic constitution of the Gp. Andigena population. These clones would stand-out and be easily selected by the farmers due to the hybrid vigor they would have shown. If we think of this phenomenon occurring over a long time period, a considerable number of clones could have arisen this way comprising a high proportion of the total Gp. Andigena population.

A fact that was observed in the present study indicated that a relatively high proportion of haploids obtained from Gp. Andigena were male fertile, while haploids from Gp. Tuberosum reported in previous studies (Peloquin and Hougas, 1958; Ross, Peloquin and Hougas, 1964) were mainly male sterile. Approximately fifty percent of the Gp. Andigena haploids were male fertile, and pollen stainability was observed to be above forty percent. Some haploid clones were comparable to their cultivated diploid relatives with regard to pollen stainability (Figures 1, 2, 3).

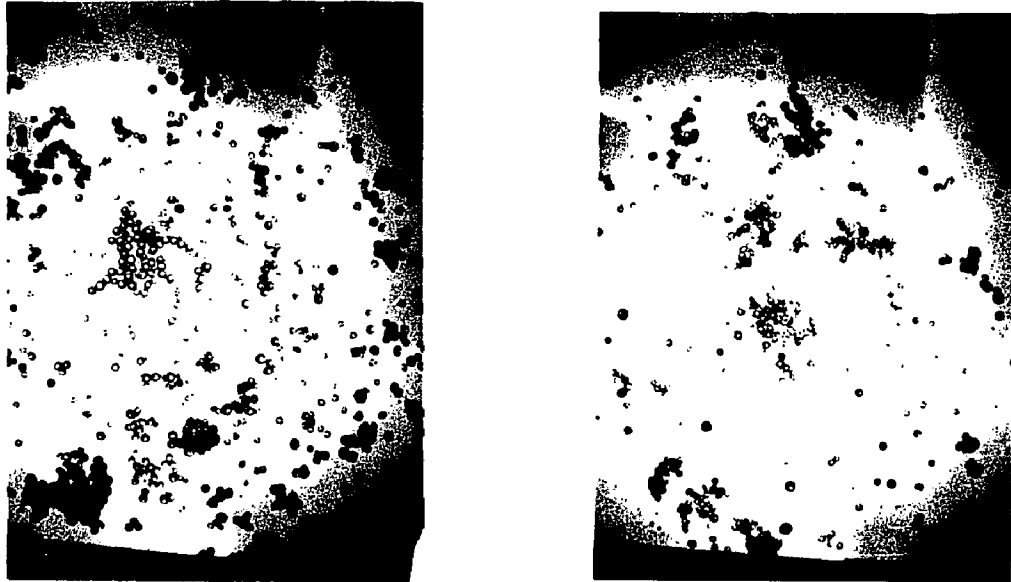
Studies of microsporogenesis, also have shown more regular meiosis in Gp. Andigena haploids than Gp. Tuberosum haploids (Yeh, Peloquin and Hougas, 1964). Because of the good male and female fertility in AH, the feasibility of building up highly fertile hybrid populations (haploid-diploid species) is encouraging, permitting the full potential of their genetic diversity to be exploited.

The crossability between AH and TH was reasonably good when AH was the male parent, but considerably less when TH was the male. By pollinating each Group with their own bulk pollen, AH x AH gave three times more seed set than TH x TH. The existence of gametophytic self-incompatibility is known in both Groups (Cipar, 1963; Cipar, Peloquin and Hougas, 1964; De la Puente, 1973), but the number of different "S" alleles probably is larger among AH than TH, because of the wider genetic base of Group Andigena.

The study of the growth of pollen tubes within the style provided evidence of the presence of self-incompatible alleles in AH. The average number of pollen tubes observed within the upper third of the style was twice as many as those within the lower third, indicating that 50% of the tubes were blocked on their way down the style, presumably because they shared common self-incompatible alleles (Figure 4). When the same AH females were crossed with PHU bulk pollen, the number of pollen tubes growing all the way down the style was considerably higher as is expressed in Table 3 (Figure 5). Apart from these average figures, the variability of pollen tube behavior among these AH clones can not be ignored. In some instances, large numbers of pollen tubes penetrated the style but failed to set seed possibly due to the production of large numbers of

2n eggs resulting in triploid embryo formation and seed abortion due to the breakdown of the pentaploid endosperm; in other instances, few pollen tubes penetrated the style yet seed set occurred, and in still other instances abundant pollen germinated but suddenly stopped growth in the style again resulting in no seed set (Figure 6). This latter type of incompatible pollen/pistil reaction is not typical of gametophytic self- or cross-incompatibility in Solanaceae, where incompatible pollen tubes gradually stop growing in the style. Nevertheless, in Oenothera organensis, a species with gametophytic incompatibility, a "stigmatic" inhibition of incompatible pollen occurs, resembling that of sporophytic incompatibility; however, incompatible pollen grains germinate on the stigma surface and pollen tubes start to penetrate the stigmatic tissue, and are then inhibited in their further growth (Dickinson and Lawson, 1975). In any event, additional experiments are needed to explain the source of these problems.

The breeding potential of the Gp. Andigena haploids is partially expressed by their crossability behavior in this study. More information is needed to fully reveal their potential. It seems likely that Gp. Andigena haploids will reach their full potential and usefulness as the development of diploid breeding stocks continues to be pursued for use in the 2n gamete approach to potato improvement.



Figures 1, 2. Pollen stainability and presence of large (2n) pollen in AH and TH bulk pollen (left to right).

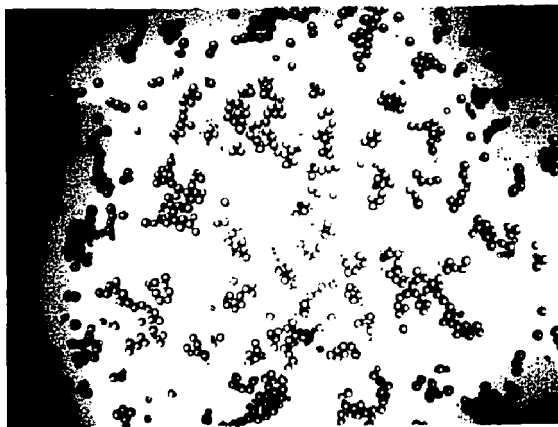


Figure 3. Pollen stainability of PHU bulk pollen.

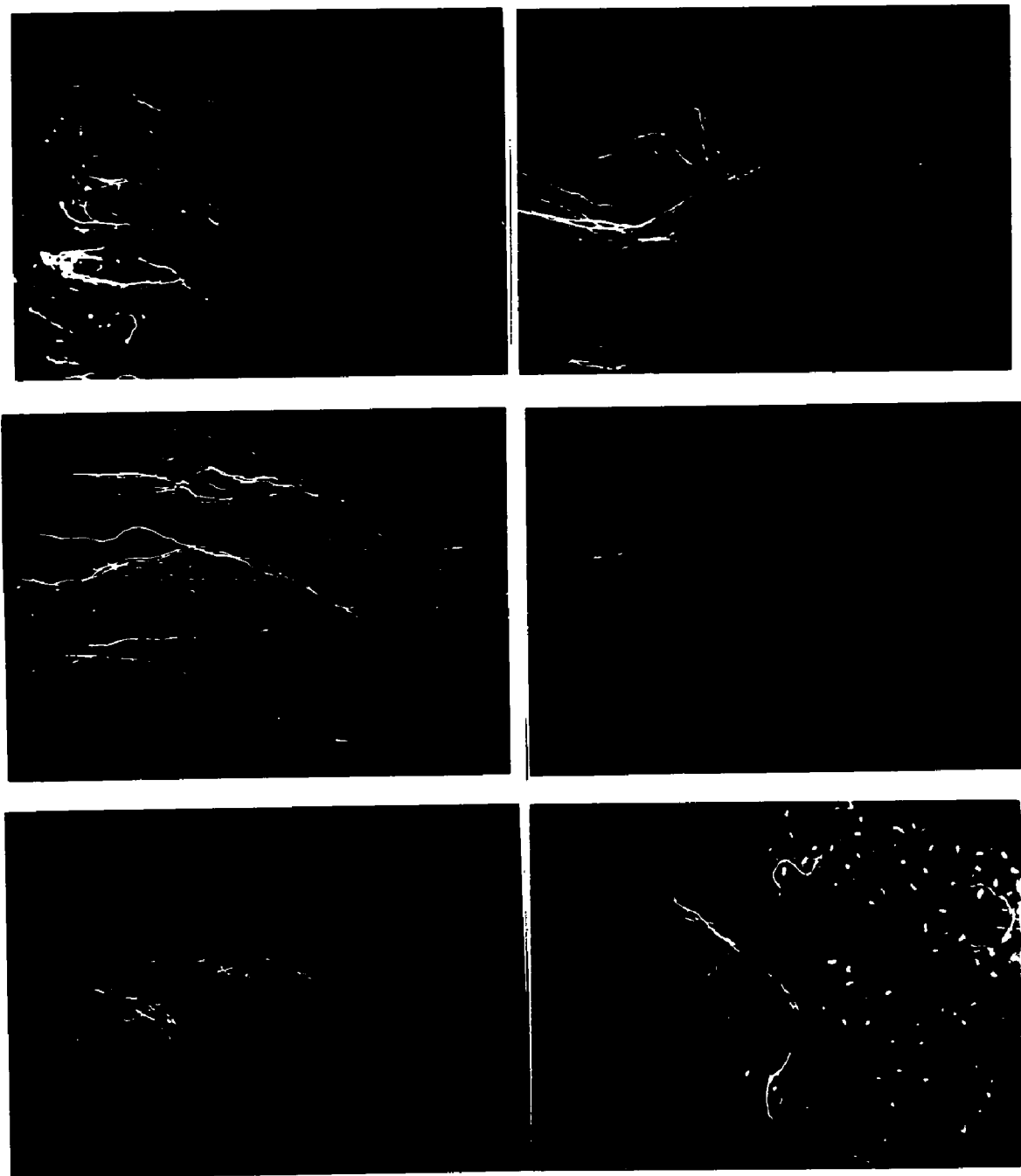


Figure 4. AH bulk pollen tube growth within the style of AH clone. Note reduction of pollen tubes as they grow down the style (upper left: stigma, lower left: bottom of style and lower right: ovary).

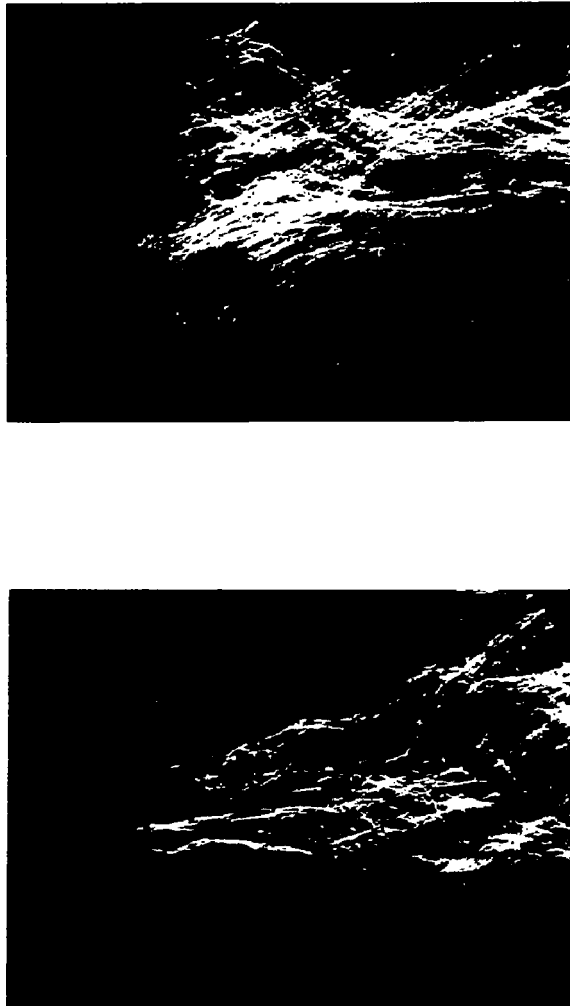


Figure 5. PHU bulk pollen on style of AH clone. Note countless pollen tubes growing down the style. Stigma region (top) and bottom of style (bottom).

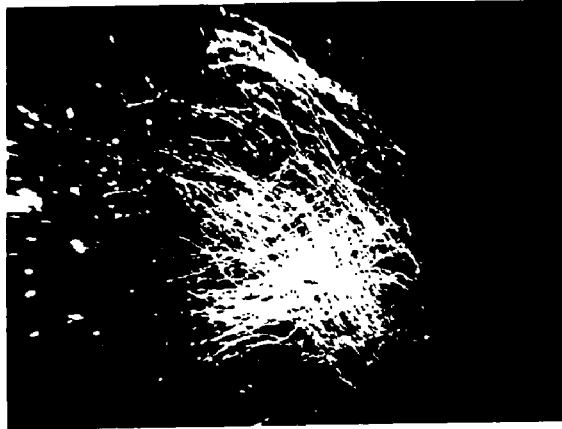


Figure 6. PHU bulk pollen on style of AH clone. Note sudden stop of pollen tube growth in the upper end of the style (beneath the stigma).

Heterosis and Gene Effects of Solanum tuberosum Gp. Andigena

Haploids in a Diallel Cross with Solanum tuberosum

Groups Phureja, Stenotomum and Tuberosum Haploids

INTRODUCTION

Along with the development of diploid populations of potatoes, whether haploids from tetraploid cultivars, diploid cultivated Groups or hybrids among them, the need for a better understanding of their genetic variation, hybrid behavior, and nature of gene action becomes mandatory. Since the improvement of techniques to increase the frequency of haploid extraction from tetraploid Groups, the analysis of quantitative variation at the diploid level has been facilitated. The tetrasomic quantitative variation usually is troublesome and models applied to it do not completely partition all the existing genetic components (Levings and Dudley, 1963).

Earlier crosses among Gp. Tuberosum cultivars and Gp. Andigena clones were done at the tetraploid level (Cubillos and Plaisted, 1976; Glendinning, 1969; Paxman, 1965; Rothacker, 1962; Tarn and Tai, 1977), seeking to widen the genetic variation of Gp. Tuberosum as well as to provide highly heterotic hybrids. The Gp. Andigena clones were unadapted to northern latitudes and the hybrid combinations with local Gp. Tuberosum cultivars did not express any heterotic advantage for total tuber yield as compared to a standard check (Rothacker, 1962), but tuber number was significantly increased. Adapted clones for tuberization under long days from Gp. Andigena, when crossed to Gp. Tuberosum advanced lines or varieties, did express heterosis for tuber

yield (Cubillos and Plaisted, 1976; Glendinning, 1969; Paxman, 1965; Tarn and Tai, 1977).

Crosses among Gp. Tuberosum and Gp. Andigena haploids, to study heterosis and breeding behavior, were not reported until now. The availability of haploid clones from both Groups would allow the study of their hybrid behavior at the diploid level.

Despite the complexity of tetrasomic inheritance of quantitative traits, general combining ability analysis (GCA), was mainly used to determine genetic variation. Results from most reports indicated a large specific combining ability (SCA) for total tuber yield, average tuber weight and average weight as marketable tuber (Plaisted and et al, 1962; Sanford, 1960; Tai, 1976). Although Tai (1976), found the variation of average weight of tubers due primarily to GCA, the GCA of yield and number of marketable tubers were significant at the 10% level. GCA was also important in determining specific gravity (Sanford, 1960; Tai, 1976).

Combining ability analysis as a tool to determine genetic variation and gene action in the expression of quantitative traits such as tuber yield, was not applied to potato haploids until now; although Rowe (1969), used Gp. Tuberosum haploids in crosses with Gp. Phureja to determine genetic variation using Design I and Design II models. Additive genetic variance was reported to be the largest component for tuber weight.

The experimental material in this study is comprised of haploids from unadapted Gp. Andigena clones; partially adapted diploid clones from Gps. Phureja and Stenotomum, and random haploids from Gp. Tuberosum

cultivars. The Group populations and Group-hybrid populations, were generated in a diallel set as described in materials and methods.

The major objectives of this study were, (1) to determine the breeding behavior of the Group populations, particularly that of Gp. Andigena; (2) to quantify the hybrid vigor of the Group-hybrids, and (3) to determine the gene action of their yield components and their heritability.

MATERIALS AND METHODS

BULK POPULATIONS

Group Andigena bulk populations.

Twenty-eight plant introductions (PI's) which represent six South and Central American countries (Argentina, Bolivia, Peru, Ecuador, Colombia and Mexico), were the source of parental clones for haploid extraction. A sample of 32 haploids from the 28 PI's, pollinated with bulk pollen obtained from themselves, were used to provide equal number of seeds to make a composite. This composite constituted the Group Andigena haploid (AH) bulk population.

Group Tuberosum bulk population.

The source of this Group came from randomly chosen haploid clones that were pollinated with bulk pollen from their own Group. A sample of 30 haploid clones, contributing an equal number of seeds, formed the Group Tuberosum haploid (TH) bulk population.

Group Phureja population.

The origin of this population traces back to 1968, where 484 clones entered selection for tuberization under long days. The selected clones were bulk pollinated to provide the seed material for the next cycle of selection. A total of three cycles of selection was carried out through 1976. Seeds from the latest cycle were the source of the Group Phureja (PHU) bulk populations.

Group Stenotomum bulk population.

Following the same procedure as that of the Phureja population, selection for tuberization under long days was carried out for Gp. Stenotomum starting in 1966. Three cycles of selection were applied up to 1976. Seeds from bulk crosses of selected clones in the third cycle were taken to constitute the Group Stenotomum (STN) bulk population.

Group-hybrid populations.

These populations included hybrids among parental Groups such as AH x STN, AH x PHU, TH x AH, TH x STN, TH x PHU. They were generated by taking individual clones from every parental Group and pollinating them with bulk pollen other than their own Group. Twenty seeds per cross from 37 AH x STN clones, 20 seeds/cross from 44 AH x PHU, 15 seeds/cross from 40 TH x AH, 15 seeds/cross from 39 TH x STN and 15 seeds/cross from 40 TH x PHU clones were bulked separately to form the Group-hybrid populations.

Seed germination and seedling handling.

Seeds from Groups and Group-hybrids were soaked in 1500 ppm. gibberellic acid for 24 hours to ensure uniformity of germination. They were rinsed with tap water and immediately sown in three inch clay pots filled with Jiffy mix and covered with vermiculite. They were kept in the greenhouse. After germination the seedlings were transplanted to individual peat pots filled with a mixture of soil and sand (3:1) and liquid fertilizer was applied. Previous to the transplanting of the seedlings to the field, they were separated in two groups and placed

in screenhouses to harden them to the environment. They were uniformly sprayed with insecticide and fertilized immediately before transplanting.

Experimental design.

The experimental design used was a randomized complete block (RCB), with three replications in two locations. Every entry was comprised of 60 individuals per replication. Plants were spaced one foot apart within the row, with four feet between rows at the University of Wisconsin (U.W.) Peninsular Branch Experiment Station at Sturgeon Bay; and three feet between rows at the U.W. Experiment Station at Hancock. The dates of seedling transplanting to the fields were, June 8th for Hancock and June 13th for Sturgeon Bay, both in 1978. Normal recommended cultural practices were followed throughout the duration of the experiment. The harvesting was carried out during the weeks of September 27th for Hancock and October 12th for Sturgeon Bay.

Data were obtained on a per plot basis and were later transformed to weight per plant.

Total tuber weight per plot and fresh vine weight per plot were taken directly in the field at harvesting time. The pooled tuber + fresh vine values were derived later by adding them on a per plot basis also.

The dry matter of vines was obtained by the following procedure: a branch of every plant within every plot was cut and placed together in a paper bag. These samples were taken for every entry and each replication separately. They were immediately weighed and later placed in a dryer at 80°F with air flow within the chambers. After three weeks the samples were removed and immediately weighed. The percent of

dry matter was obtained and used to calculate the total vine dry matter on a per plot basis. Later a mean dry matter in pounds per plant was determined.

The total dry matter was obtained by pooling vine dry matter and tuber dry matter. The percent of dry matter of tubers was obtained directly from Maercker's table (Behrend et al, 1880) which is widely used. It is derived from the specific gravity and is highly correlated with the actual dry matter extraction (Schippers, 1976). Once the dry matter of tubers was obtained, it was used to calculate the yield of tuber dry matter per plant and then added to vine dry matter to get the total dry matter per plant.

The specific gravity was determined from tuber samples taken per plot. The tuber sampling was done by picking up one tuber per plant. Weight of tubers in the air divided by weight in air minus weight in water (wt. air/wt. air - wt. water), was used to determine the specific gravity values.

The analysis of variance for combining ability was done on an entry-mean basis. A computer program set up according to a general least square analysis for a general (unbalanced) diallel experiment (Schaffer and Usanis, 1969), was used. Griffing's method-2 model-2 (Griffing, 1956), was essentially followed (parents and one set of F_1 's were included but not reciprocal F_1 's).

RESULTS AND DISCUSSION

HETEROSIS

The present study suggests heterosis among inter-Group potato populations as reported elsewhere in corn open-pollinated cultivars (Richey, 1922; Robinson et al, 1955, 1956; Lonnquist and Gardner, 1961). However, most F_1 hybrid means, particularly AH F_1 's, were not significantly different for most traits. Trends or differences that were observed, we believe, have biological meaning since highly variable populations are compared.

Total tuber yield.

The AH F_1 hybrids had higher tuber yield than the constant AH parent, but this performance was not any better than any of the alternative parents in neither of the two locations nor the combined (Tables 1, 2, 3). However, the pooled AH F_1 means showed 15.6% heterosis over the mid-parent of location 1 (Sturgeon Bay) (Table 4), and did not go over the highest parent, but was 184.6% better than the constant AH parent. At location 2 (Hancock), no heterosis was evident, but there was 10.7% improvement over the constant AH parent (Table 5). In the combined, the percent of heterosis over the mid-parent was not significant (1.5%); however, tuber yield was improved 65.9% over the parental AH Group (Table 6).

The TH F_1 hybrids, except for TH x AH, had higher tuber yield than both parents at location 1 and the combined (Table 1, 3). At location 2, only TH x STN had higher yield than both parents. TH x PHU was only higher than PHU (Table 2). The pooled TH F_1 means indicated

heterosis over the mid- and highest parent at location 1 (Table 4); however, at location 2 heterosis was evident only over the mid-parent (Table 5). In the combined, these F_1 means were 34.4% higher than the mid-parent and only 2.4% over the highest parent (Table 6).

The pooled F_1 means for STN and PHU, separately, were higher than the mid- and highest parent in both locations and the combined (Tables 4, 5, 6), except for the PHU F_1 mean over the highest parent at location 2 which was lower. In either case tuber yield was greatly increased compared to the constant parents STN and PHU.

Fresh vine yield.

One of the main reasons vine yield was measured, was to add it to the total tuber weight so that the total plant accumulation could be determined, and perhaps best assess any heterotic advantage of the hybrids, since tuberization per se in South America potatoes is highly affected by long daylengths and high temperatures (Mendoza and Haynes, 1977). A second reason was to obtain the dry matter of the vines, so that it could be added to the tuber dry matter to get the total dry matter yield.

In contrast to tuber yield, AH F_1 hybrids in general did not out-yield the constant AH parent for fresh vine, but they had higher yields than the alternative parents in both locations and the combined (Tables 1, 2, 3). The only exception was AH x PHU which had slightly higher fresh vine yield than the constant AH parent over all locations. Heterosis of the pooled AH F_1 means, was not expressed at any of the two locations nor the combined (Tables, 4, 5, 6).

The TH F_1 hybrids, except for AH x TH, had fresh vine yield as follows: TH x STN was higher than both parents at location 1 and the combined; however at location 2, it was higher than STN but lower than TH. TH x PHU had higher vine yield than the constant parent at both locations and the combined, but lower than the alternative parents (Tables 1, 2, 3). Heterosis of the pooled TH F_1 means was only expressed over the mid-parent at location 1 (2.9%), but none at location 2 nor the combined (Tables 4, 5, 6).

The pooled STN F_1 means had 2.4%, 1.7% and 2.1% higher, fresh vine yield, than the mid-parent at location 1, location 2 and the combined respectively. The pooled PHU F_1 means expressed heterosis over the mid- and higher parent over all locations (Tables 4, 5, 6).

Tuber + fresh vine yield.

The AH F_1 hybrids at location 1 (Table 1), particularly AH x TH and AH x STN, were not any higher than the constant parent AH; but, they were higher than the alternative parents TH and STN. However, AH x PHU was higher than both parents at this location. At location 2 (Table 2), none of the AH hybrids outyielded the constant AH and, AH x TH was over lower than both parents; however, AH x STN and AH x PHU were higher than the alternative parents STN and PHU respectively. In the combined (Table 3), AH x TH had lower yield than both parents. AH x STN was lower than the constant AH but higher than the alternative STN. AH x PHU was higher than both parents. Heterosis expressed by the pooled AH F_1 means over the mid- and the highest parent was about

2% at location 1 (Table 4). There was no heterosis in location 2 nor the combined (Tables 5, 6).

The TH F_1 hybrids, TH x STN and TH x PHU, had higher yields than both parents in both locations and the combined (Tables 1, 2, 3). Heterosis of the pooled TH F_1 means was 12.7% over the mid-parent and 7.1% over the highest parent at location 1 (Table 4). At location 2, it was 2.8% over the mid-parent and none over the highest parent (Table 5). In the combined, heterosis was expressed as 9.5% over both the mid- and highest parent (Table 6).

Heterosis of the pooled F_1 means for STN and PHU was as follows; STN F_1 had 1.8% and 1.1% heterosis over the mid- and highest parent respectively; whereas the PHU F_1 mean expressed 9.1% and 3.3% heterosis over the mid- and highest parent respectively at location 1 (Table 4). At location 2, heterosis was 15.8% and 3.4% over the mid-parent for STN and PHU F_1 means respectively (Table 5). None of them expressed heterosis over the highest parent. In the combined, both STN and PHU F_1 means outyielded the mid- and highest parent with percentages of heterosis being 12.9%, 8.1%, respectively for STN, and 7.3%, 6.5% for PHU, respectively (Table 6).

Dry vine yield.

The dry vine weight for AH F_1 hybrids yielded more than both parents for AH x STN and AH x PHU at location 1 (Table 1). AH x TH was lower than AH but higher than TH. Heterosis of the pooled AH F_1 means was 12.0% and 7.7% over the mid- and highest parent, respectively at location 1 (Table 4). At location 2, none of the AH hybrids had higher

yields than the constant AH parent, but they were higher than the alternative parents except TH (Table 2). Heterosis of the pooled AH F_1 means at this location was not observed (Table 5). In the combined, only AH x PHU was higher than both parents. The rest of the AH hybrids were the same or lower than the constant AH parent, but higher than the alternative parents (Table 3). Heterosis in the combined was only expressed over the mid-parent by the pooled AH F_1 means (Table 6).

The TH F_1 hybrids at location 1, had higher vine dry matter yield than TH, but lower than the alternative parents AH, STN and PHU (Table 1). Almost no heterosis was observed for the pooled TH F_1 means at this location (Table 4). At location 2, TH hybrids were not any better than either parent, consequently no heterosis was observed (Table 2, 5). In the combined, TH x PHU was higher than TH but lower than PHU; TH x AH was higher than TH but lower than AH, and TH x STN was lower than both parents (Table 3). Heterosis was not observed in the combined by the pooled TH F_1 means (Table 6).

The pooled F_1 means for STN and PHU demonstrated heterosis over their mid-parents at location 1 (Table 4). No heterosis was observed with either Group at location 2 (Table 5). In the combined, the pooled STN F_1 mean was 5.6% higher than the mid-parent and, the pooled PHU F_1 mean did not express any heterosis (Table 6).

Total dry matter (tuber + vine).

Total dry matter for AH F_1 hybrids at location 1 was higher than either parent (Table 1). The heterotic advantage of the pooled AH F_1 means over the mid-parent was 14.3% and 7.9% over the highest parent at

this location (Table 4). At location 2, AH hybrids did not have higher total dry matter yields than the constant AH parent, nor did AH x TH over TH, but they were higher than the alternative parents STN and PHU. No heterosis was expressed in this location by the pooled AH F_1 means (Table 5). In the combined AH hybrids had equal or higher dry matter yields than the constant AH parent and alternative parents STN and PHU, but lower than TH (Table 3). The pooled AH F_1 means had 5.9% more dry matter yield than the mid-parent and 3.8% more than the highest parent in the combined (Table 6).

The TH F_1 hybrids at location 1, except TH x AH, had higher total dry matter yields than their parents (Table 1). The percent of heterosis of the pooled TH F_1 means at this location was 12.4% over the mid-parent and 7.9% over the highest parent (Table 4). At location 2, from TH hybrids, except TH x AH, only TH x STN was slightly higher than both parents; TH x PHU was lower than TH but higher than PHU (Table 2). The pooled TH F_1 means had 2.3% higher yield than the mid-parent at this location (Table 5). In the combined, with the exception of TH x AH, both TH x STN and TH x PHU hybrids, had higher yields than both of their respective parents (Table 3), and the heterosis expressed by the pooled TH F_1 means was 7.5% over the mid-parent and 5.6% over the highest parent respectively (Table 6).

Heterosis of the pooled STN F_1 means at location 1 was 17.4% higher than the mid-parent and 10.9% over the highest parent. The pooled PHU F_1 means were 13.6% and 4.4% over the mid- and highest parent respectively at this location (Table 4). At location 2, the pooled STN F_1 means had 15% heterosis only over the mid-parent; likewise the pooled

PHU F_1 means was 4.8% greater than the mid-parent (Table 5). In the combined, the STN F_1 mean was 15.7% higher than the mid-parent and 13.5% greater than the highest parent. The PHU F_1 mean was 9.4% higher than both the mid- and the highest parent (Table 6).

Specific gravity.

Although specific gravity served as a source to determine tuber dry matter, a few remarks can be made about its heterotic behavior.

AH F_1 hybrids, except AH x PHU, had higher specific gravity than their both parents at both locations and the combined (Tables 1, 2, 3). However, AH x PHU at location 1 had equal specific gravity to AH but higher than PHU, and lower than AH but higher than PHU at location 2 as well as in the combined. Heterosis was less than 1% over the mid- and highest parent over all locations for the pooled AH F_1 means (Tables 4, 5, 6).

TH F_1 hybrids at location 1 except TH x AH, were as follows: TH x STN had higher specific gravity than TH but not than STN; conversely TH x PHU was lower than TH but higher than PHU (Table 1). At location 2 and the combined, TH x STN values were higher than either parent and TH x PHU lower than TH but higher than PHU (Tables 2, 3). Heterosis expressed by the pooled TH F_1 means, was less than 1% over the mid- and highest parent over all locations (Tables 4, 5, 6).

The pooled F_1 means of STN and PHU, were less than 1% or zero over the mid- and highest parent over all locations (Tables 4, 5, 6).

Discussion.

Although the detrimental effect of long daylength and high temperatures was known on tuber initiation and tuber development among the short-day cultivated South American potatoes (Alvey, 1963; Burt, 1964; Ewing, 1978; Mendoza and Haynes, 1976, 1977; Slater, 1968), Groups AH, STN and PHU increased tuberization dramatically in a hybrid state. Even when AH was crossed to STN and PHU, which had undergone three cycles of selection for tuberization, AH tuberization was improved as judged by tuber yield performance. The maximum hybrid vigor, expected from tuber yield, undoubtedly was penalized because of the unfavorable photoperiodic response, as was shown when AH was one of the parents. Even so, when PHU and STN were hybridized with TH, they expressed heterosis over the mid-parent at all locations. Besides, at location 2, the yield of TH x STN was even higher than both parents. The shortening of the daylight by the end of the growing season, may have helped tuberization of the South American Groups, giving them a chance to catch up with TH.

Fresh vine yield, was not much help in elucidating the hybrid vigor of AH hybrids, except for the individual performance of AH x PHU. However, the pooled AH F_1 means failed to demonstrate heterosis over the mid-parent and the highest parent over all locations. Biologically, the lack of heterosis of the AH hybrids for vine growth, can be interpreted as being less efficient in accumulation and or use of photosynthates in the aerial parts than the AH parent, although they were higher than the alternative parents. The apparent efficiency of the AH parent comes from its critical daylength for tuberization, which

seems to be shorter than its hybrids; therefore vine growth under long daylengths was predominant. Contrarily, AH hybrids whose alternative parents had undergone selection for tuberization for several cycles, may have started initiating stolons and tubers; therefore, the total vine growth was reduced compared to AH. These hybrids produced more vine growth than the alternative parents. This can be explained by the response of the critical daylength for tuberization of the partially adapted and adapted Groups that were crossed to the unadapted AH, promoting increased vine growth.

In regard to effect of the TH hybrids, on the pooled F_1 mean basis, almost no heterosis for fresh vine yield was detected, over the mid-parents except at location 1 (2.9%). However, as individual hybrid Group performances, TH x STN went slightly over both parents in vine yield at location 1 and the combined. The other two hybrids did not outyield the alternative parents AH and PHU; although they were higher than the constant parent (TH), except at location 2.

The tendency of hybrids between semiadapted and unadapted Groups to produce more vine growth than hybrids between adapted and semiadapted Groups is probably a function of the balance of genes for tuberization and vine growth. It is likely that growth regulators and other organic substances related to tuber and foliage development under long daylengths were more balanced among unadapted x adapted hybrids than among unadapted x semiadapted hybrids; therefore, the vine growth response was greater as the material approaches unadaptation for tuberization.

The total fresh weight accumulation (tubers + vine) particularly for AH and its hybrids, paralleled vine yield performance. Conversely,

TH hybrids, as a pooled F_1 mean did express heterosis over the mid-parent over all locations, and over the highest parent at location 1 and the combined. The single TH Group-hybrid performances, with the exception of TH x AH, in general had higher yields than both parents. Apparently what caused heterosis to be expressed, is the input of vines more than tubers on the total accumulation.

The vine dry matter was variable, but comparable to fresh vine performance for AH hybrids, except for the switch of AH x STN at location 1. The TH hybrids vine dry matter yield, remained close to their fresh vine performance.

The total dry matter accumulation (tuber + vine), at location 1 for AH hybrids was higher than both parents. Perhaps the compensation of each (tuber and vine) during the total development of the plant resulted in the total dry matter output being greater for the AH hybrids than their parents, demonstrating heterosis in this particular environment. At location 2 the total dry matter yield of the AH hybrids was not any higher than AH, where again the dry vine input was providing the differences. Conversely, the TH hybrids had all higher yields than both parents with the exception of TH x AH at location 1. At location 2, only TH x STN had higher yields than both parents. Again the contribution of tuber or vine to the accumulation of total dry matter would establish the differences among TH and its hybrids according to their compensation rate.

In regard to specific gravity, apparently on the population basis, heterosis was not expressed upon Group hybridizations. However, variability was observed within Groups and Group-hybrids. In general,

Table 1. Mean yields (tuber, vine, tuber + vine, dry vine, total solids in lbs/hill, and specific gravity) of the parental Groups (diagonal) and their F_1 intercross combinations (location 1, Sturgeon Bay).

	AH	TH	STN	PHU	F_1 Means
AH					
total tuber wt.	.26	.93	.78	.50	.74
fresh vine wt.	4.31	3.48	3.76	4.49	3.91
tuber + vine wt.	4.57	4.47	4.55	4.99	4.67
dry vine wt.	.52	.48	.58	.62	.56
total dry matter wt.	.56	.63	.71	.70	.68
specific gravity	1.061	1.068	1.070	1.061	1.066
TH					
total tuber wt.		1.20	1.79	1.44	1.39
fresh vine wt.		2.98	3.51	3.69	3.56
tuber + vine wt.		4.18	5.30	5.13	4.97
dry vine wt.		.39	.41	.48	.46
total dry matter wt.		.58	.71	.71	.68
specific gravity		1.064	1.066	1.061	1.065
STN					
total tuber wt.			.99	-	1.29
fresh vine wt.			3.46	-	3.64
tuber + vine wt.			4.45	-	4.50
dry vine wt.			.47	-	.50
total dry matter wt.			.64	-	.71
specific gravity			1.068	-	1.068
PHU					
total tuber wt.				.88	.97
fresh vine wt.				4.02	4.09
tuber + vine wt.				4.90	5.06
dry vine wt.				.56	.55
total dry matter wt.				.68	.71
specific gravity				1.053	1.061

Table 2. Mean yields (tuber, vine, tuber + vine, dry vine, total solids in lbs/hill and specific gravity) of the parental Groups (diagonal), and their F_1 intercross combinations (location 2, Hancock).

	AH	TH	STN	PHU	F_1 Means
AH					
total tuber wt.	.56	.74	.61	.52	.62
fresh vine wt.	1.64	.94	1.34	1.68	1.32
tuber + vine wt.	2.20	1.68	1.95	1.95	1.86
dry vine wt.	.33	.22	.27	.32	.27
total dry matter wt.	.43	.36	.39	.41	.39
specific gravity	1.073	1.077	1.076	1.070	1.074
TH					
total tuber wt.		1.27	1.51	1.17	1.14
fresh vine wt.		1.10	1.07	1.16	1.06
tuber + vine wt.		2.36	2.58	2.32	2.19
dry vine wt.		.26	.23	.25	.23
total dry matter wt.		.50	.52	.47	.45
specific gravity		1.076	1.078	1.073	1.076
STN					
total tuber wt.			.63	-	1.06
fresh vine wt.			1.00	-	1.21
tuber + vine wt.			1.64	-	2.27
dry vine wt.			.21	-	.25
total dry matter wt.			.33	-	.46
specific gravity			1.074	-	1.077
PHU					
total tuber wt.				.58	.85
fresh vine wt.				1.26	1.42
tuber + vine wt.				1.85	2.14
dry vine wt.				.30	.29
total dry matter wt.				.37	.44
specific gravity				1.060	1.072

Table 3. Mean yields (tuber, vine, tuber + vine, dry vine, total solids in lbs/hill and specific gravity) of the parental Groups (diagonal) and their F_1 intercross combinations (2 locations, combined).

	AH	TH	STN	PHU	F_1 Means
AH					
total tuber wt.	.41	.84	.70	.51	.68
fresh vine wt.	2.98	2.21	2.55	3.09	2.62
tuber + vine wt.	3.39	3.08	3.25	3.47	3.27
dry vine wt.	.43	.35	.43	.47	.42
total dry matter wt.	.50	.50	.55	.56	.54
specific gravity	1.067	1.073	1.073	1.066	1.071
TH					
total tuber wt.		1.24	1.65	1.31	1.27
fresh vine wt.		2.04	2.29	2.43	2.31
tuber + vine wt.		3.27	3.94	3.73	3.58
dry vine wt.		.33	.32	.37	.35
total dry matter wt.		.54	.62	.59	.57
specific gravity		1.070	1.072	1.067	1.071
STN					
total tuber wt.			.81	-	1.18
fresh vine wt.			2.23	-	2.42
tuber + vine wt.			3.05	-	3.60
dry vine wt.			.34	-	.38
total dry matter wt.			.49	-	.59
specific gravity			1.071	-	1.073
PHU					
total tuber wt.				.73	.91
fresh vine wt.				2.64	2.76
tuber + vine wt.				3.38	3.60
dry vine wt.				.43	.39
total dry matter wt.				.53	.58
specific gravity				1.061	1.067

Table 4. Yield of parental Groups and their average F_1 mean together with the F_1 mean expressed as a percent of the mid-parent, high parent, and constant parent yields (location 1, Sturgeon Bay).

PARENTAL GROUP	YIELD IN LBS/HILL		MEAN F_1 % RELATIVE TO		
	Constant Parent	Pooled F_1 Mean	Mid Parent	High Parent	Constant Parent
AH					
total tuber wt.	.26	.74	115.6	72.5	284.6
fresh vine wt.	4.31	3.91	100.3	90.7	90.7
tuber + vine wt.	4.57	4.67	102.9	102.2	102.2
dry vine wt.	.52	.56	112.0	107.7	107.7
total dry matter wt.	.56	.68	114.3	107.9	121.4
specific gravity	1.061	1.066	100.4	100.5	100.5
TH					
total tuber wt.	1.20	1.39	144.8	115.8	115.8
fresh vine wt.	2.98	3.56	102.9	90.6	119.5
tuber + vine wt.	4.18	4.97	112.7	107.1	118.9
dry vine wt.	.39	.46	102.2	88.5	117.9
total dry matter wt.	.58	.68	112.4	107.9	117.2
specific gravity	1.064	1.065	100.3	100.1	100.1
STN					
total tuber wt.	.99	1.29	150.0	130.3	130.3
fresh vine wt.	3.46	3.64	102.4	99.7	105.2
tuber + vine wt.	4.45	4.50	101.8	101.1	101.1
dry vine wt.	.47	.50	106.4	106.4	106.4
total dry matter wt.	.64	.71	117.4	110.9	110.9
specific gravity	1.068	1.068	100.2	100.0	100.0
PHU					
total tuber wt.	.88	.97	119.8	110.2	110.2
fresh vine wt.	4.02	4.09	106.5	101.7	101.7
tuber + vine wt.	4.90	5.06	109.1	103.3	103.3
dry vine wt.	.56	.55	107.8	98.2	98.2
total dry matter wt.	.68	.71	113.6	104.4	104.4
specific gravity	1.053	1.061	100.5	99.8	100.8

Table 5. Yield of parental Groups and their F_1 mean together with the F_1 mean expressed as a percent of the mid-parent, high parent, and constant parent yields (location 2, Hancock).

PARENTAL GROUP	YIELD IN LBS/HILL		MEAN F_1 % RELATIVE TO		
	Constant Parent	Pooled F_1 Mean	Mid Parent	High Parent	Constant Parent
AH					
total tuber wt.	.56	.62	89.2	74.7	110.7
fresh vine wt.	1.64	1.32	95.7	80.5	80.5
tuber + vine wt.	2.20	1.86	89.4	84.5	84.5
dry vine wt.	.33	.27	91.5	81.8	81.8
total dry matter wt.	.43	.39	94.0	90.7	90.7
specific gravity	1.073	1.074	100.2	100.1	100.1
TH					
total tuber wt.	1.27	1.14	122.6	89.8	89.8
fresh vine wt.	1.10	1.06	88.3	81.5	81.5
tuber + vine wt.	2.36	2.19	102.8	92.8	92.8
dry vine wt.	.26	.23	85.2	82.1	82.1
total dry matter wt.	.50	.45	102.3	90.0	90.0
specific gravity	1.076	1.076	100.3	100.0	100.0
STN					
total tuber wt.	.63	1.06	135.9	115.2	168.3
fresh vine wt.	1.00	1.21	101.7	88.3	121.0
tuber + vine wt.	1.64	2.27	115.8	99.6	138.4
dry vine wt.	.21	.25	96.2	83.3	119.0
total dry matter wt.	.33	.46	115.0	97.9	139.4
specific gravity	1.074	1.077	100.2	100.2	100.3
PHU					
total tuber wt.	.58	.85	113.3	92.4	146.6
fresh vine wt.	1.26	1.42	107.6	103.6	112.7
tuber + vine wt.	1.85	2.14	103.4	93.9	115.7
dry vine wt.	.30	.29	96.7	96.7	96.7
total dry matter wt.	.37	.44	104.8	93.6	118.9
specific gravity	1.060	1.072	100.4	99.7	96.7

Table 6. Yield of parental Groups and their F_1 mean together with the F_1 mean expressed as a percent of the mid-parent, high parent, and constant parent yields (combined locations 1 and 2).

PARENTAL GROUP	YIELD IN LBS/HILL		MEAN F_1 % RELATIVE TO		
	Constant Parent	Pooled F_1 Mean	Mid Parent	High Parent	Constant Parent
AH					
total tuber wt.	.41	.68	101.5	73.1	165.9
fresh vine wt.	2.98	2.62	99.2	87.9	87.9
tuber + vine wt.	3.39	3.27	98.8	96.5	96.5
dry vine wt.	.43	.42	105.0	97.7	97.7
total dry matter wt.	.50	.54	105.9	103.8	108.0
specific gravity	1.067	1.071	100.4	100.4	100.0
TH					
total tuber wt.	1.24	1.27	134.4	102.4	102.4
fresh vine wt.	2.04	2.31	99.1	88.2	113.2
tuber + vine wt.	3.27	3.58	109.5	109.5	109.5
dry vine wt.	.33	.35	95.9	87.5	106.1
total dry matter wt.	.54	.57	107.5	105.6	105.6
specific gravity	1.070	1.071	100.3	100.1	100.1
STN					
total tuber wt.	.81	1.18	143.9	142.2	145.7
fresh vine wt.	2.23	2.42	102.1	96.4	108.5
tuber + vine wt.	3.05	3.60	112.9	108.1	118.0
dry vine wt.	.34	.38	105.6	100.0	111.8
total dry matter wt.	.49	.59	115.7	113.5	120.4
specific gravity	1.071	1.073	100.3	100.2	100.2
PHU					
total tuber wt.	.73	.91	116.7	109.6	124.7
fresh vine wt.	2.64	2.76	107.2	104.5	104.5
tuber + vine wt.	3.38	3.60	107.3	106.5	106.5
dry vine wt.	.43	.39	96.3	90.7	90.7
total dry matter wt.	.53	.58	109.4	109.4	109.4
specific gravity	1.061	1.067	100.2	99.8	100.6

specific gravities were higher at Hancock than Sturgeon Bay. This is to be expected since senescence started earlier at Hancock than at Sturgeon Bay; therefore, more mature tubers were more likely to have been sampled at Hancock.

COMBINING ABILITY ANALYSIS

In the combining ability analysis of variance summarized in Tables 7, 8 and 9, it is striking to see that the specific combining ability (SCA) mean squares for all traits in all locations were not significant. Conversely GCA mean squares for all traits in location 2 were significant (Table 8). At location 1, GCA mean squares for total tuber wt., fresh vine wt., dry vine wt., and specific gravity were significant, but tuber + vine wt. and total dry matter wt. were not (Table 7). In the combined, GCA's for all traits but tuber + vine and total dry matter were significant. The interaction of GCA x locations was also significant for total tuber and total dry matter wt. (Table 9).

The estimated components of variance, σ_{gca}^2 and σ_{sca}^2 , had the same relationship as the total variances due to GCA and SCA. In location 1, the greater σ_{gca}^2 for total tuber, fresh vine, dry vine, total dry matter and specific gravity indicates the dominant role of additive-type of gene action. The pooled tuber + vine and total dry matter wt. did not have significant GCA's. It was noticed though, that the error variances were high. In location 2, the σ_{gca}^2 's for all traits were high, indicating again the preponderance of additive gene action. In the combined locations (Table 12), once again high σ_{gca}^2 's were found for total tuber, fresh vine, dry vine and specific gravity. Additive

gene action is important in these traits; however, tuber + vine and total dry matter which did not have significant GCA mean squares, did not have high σ_{gca}^2 's either. The σ_{sca}^2 's for these two traits, were not any higher than the σ_{gca}^2 's, so it can not be attributed to the importance of non-additive gene action. However, when the σ_{gca}^2 component was broken down, it could be seen that the interaction $\sigma_{gca}^2 \times \text{location}$ was greater than σ_{gca}^2 for these two traits. Besides, the interaction GCA $\times$ location mean square for total dry matter was significant, indicating that it might be the major contributor to the main source of GCA variation. Although it can not be forgotten that the error variance (σ_E^2) is also high and might reduce the power of the significance test to detect small differences in both traits.

Table 13 provides the GCA effects and variances of the parental Groups. It can be noticed that TH had significantly greater combining ability than STN and PHU for total tuber weight in all locations and the combined. STN was also higher than PHU. There was a negative GCA for AH. For fresh vine, the highest GCA effects in all locations and the combined belonged to PHU and AH. STN and TH were lower and followed in that order. GCA effects for tuber + vine were in the following order: at location 1 PHU, STN, TH, AH; at location 2 STN, TH, PHU, AH and in the combined STN, PHU, TH, AH. Vine dry matter GCA effects were in the following order: at location 1 AH, PHU, STN, TH; at location 2 PHU, AH, STN, TH and in the combined AH, PHU, STN, TH. Total dry matter GCA effects had the following order: at location 1 STN, PHU, TH, AH; at location 2 STN, TH, PHU, AH and in the combined STN, PHU, TH, AH. The GCA variances of the parental Groups obtained from the GCA effects

followed the same general order given for these effects in regard to amount for all traits in all locations. It indicates that according to the amount of their additive variances measured by GCA variances, they will transmit in that proportion their yielding ability to all their F_1 progenies.

The array mean yield performances for all traits and all Groups in both locations and the combined were ranked and compared to that of the GCA effects (Table 13). It is known that the mean yield performances are direct estimates based on no assumptions, and they provide more accurate information regarding general and specific combining ability of the Groups. It is interesting to note that the positions occupied by the parental Groups, under these two criteria of comparison, were almost the same in both locations and the combined.

Finally, heritability values for all traits in both locations and the combined are presented in Tables 10, 11 and 12. The heritability for total tuber weight is relatively high in all cases. Fresh vine yield heritabilities are under 50%. Tuber + vine heritabilities are: zero at location 1, 37.2% at location 2 and 4% in the combined. In this last instance if the interaction $\sigma_{gca}^2 \times \text{loc.}$ (Table 12) is examined, one notes that this component is greater than the main source σ_{gca}^2 . This indicates that the total σ_{gca}^2 is mainly composed of the interaction component ($\sigma_{gca}^2 \times \text{loc.}$), making the absolute σ_{gca}^2 very small. If we add both σ_{gca}^2 and $\sigma_{gca}^2 \times \text{loc.}$, the heritability estimates is boosted up to 30.9%. The vine dry matter heritability values were, 52.2% at location 1, 42.8% at location 2 and 57.3% in the combined. Total dry matter had heritabilities such as 21.5% at

location 1, 38% at location 2 and 18.4% in the combined. Again for this trait with the low heritability observed in Table 12, $\sigma^2_{gca} \times loc.$ is greater than σ^2_{gca} , indicating that it is the major contributor to the main source σ^2_{gca} . When both $\sigma^2_{gca} \times loc.$ and σ^2_{gca} are added up, the heritability for this trait is raised to 64.7%. Heritability for specific gravity was 63.8% at location 1, 56.2% at location 2 and 70.3% in the combined. These heritability values for specific gravity are in agreement with most estimates reported for this trait (Tai, 1976; Lamm, 1976, Sanford, 1960).

Discussion.

The purpose of the present diallel analysis was (1) to determine the best combiners for general and specific purposes and, (2) to provide estimates of GCA and SCA variances. It was demonstrated in the present study, that the variance components due to GCA (σ^2_{gca}) were greater than those due to SCA (σ^2_{sca}) for total tuber weight, fresh vine weight, vine dry matter weight, total dry matter weight and specific gravity, indicating the predominance of additive gene action. This would imply that simple selection schemes that make use of general combining ability effects to bring about desired changes in yield for all traits would be effective. On the other hand, the pooled tuber + vine σ^2_{gca} component was lower than σ^2_{sca} at location 1, but this last σ^2_{sca} component, was also relatively small, since both GCA and SCA mean squares were not statistically significant. At location 2, σ^2_{gca} was greater than σ^2_{sca} ; perhaps the additive gene action is better expressed in this particular location. However, in the combined, σ^2_{sca} for tuber + vine was

Table 7. Combining ability analysis of variance for six quantitative traits (location 1, Sturgeon Bay).

SOURCE	D.F.	MEAN SQUARES					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
GCA	3	1.141**	1.120*	.248	31 x 10** -1	95 x 10 -2	16 x 10** -3
SCA	1	.003	.230	.285	68 x 10 -3	21 x 10 -3	14 x 10 -4
Error	14	.023	.281	.244	38 x 10 -2	41 x 10 -2	98 x 10 -5
Total	25						
Mean =		.965	3.784	4.752	.505	.66	1.063
% CV. =		15.9	14.0	10.4	12.2	9.7	.3

* significant 5%
** significant 1%

Table 8. Combining ability analysis of variance for six quantitative traits (location 2, Hancock).

SOURCE	D.F.	MEAN SQUARES					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
GCA	3	.919**	.283**	.263**	10 x 10 ⁻¹	16 x 10 ⁻¹	24 x 10 ⁻³
SCA	1	.048	.033	.001	4 x 10 ⁻⁴	37 x 10 ⁻²	12 x 10 ⁻⁴
Error	16	.018	.032	.044	16 x 10 ⁻²	21 x 10 ⁻²	21 x 10 ⁻⁴
Total	27						
Mean =		.822	1.229	2.050	.269	.42	1.073
% CV. =		16.2	14.6	10.2	14.8	10.9	.4
* significant 5%							
** significant 1%							

Table 9. Combining ability analysis of variance six quantitative traits for the combined locations.

SOURCE	D.F.	MEAN SQUARES					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
LOC	1	.267	84.748	94.744	.727	.757	11×10^{-2}
GCA	3	2.218**	1.238**	.211	34×10^{-1}	10×10^{-1}	38×10^{-3} **
SCA	1	.034	.044	.155	60×10^{-3}	11×10^{-2}	26×10^{-4}
GCA x LOC	3	.121**	.234	.313	55×10^{-2}	15×10^{-1}	19×10^{-4}
Error	35	.022	.139	.136	27×10^{-2}	36×10^{-2}	15×10^{-4}
Total	52						
Mean =		.894	2.507	3.401	.387	.54	1.068
% CV. =		16.6	14.9	10.8	13.3	11.2	.4
* significant 5%							
** significant 1%							

Table 10. Combining ability components of variance and narrow sense heritability for six quantitative traits (location 1, Sturgeon Bay).

	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ^2_{sca}	-.0067	-.0171	.0138	-10 x 10 ⁻²	-39 x 10 ⁻²	14 x 10 ⁻⁵
σ^2_{gca}	.0947	.0658	-.0025	21 x 10 ⁻²	64 x 10 ⁻³	99 x 10 ⁻⁵
σ^2_{Error}	.0235	.2810	.2438	38 x 10 ⁻²	47 x 10 ⁻²	98 x 10 ⁻⁵
h^2	.889	.318	.000	.522	.215	.638

Table 11. Combining ability components of variance and narrow sense heritability for six quantitative traits (location 2, Hancock).

	Fresh					
	Total Tuber Wt.	Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ^2_{sca}	.0077	.0003	-.0433	-5 x 10 ⁻³	51 x 10 ⁻³	30 x 10 ⁻⁵
σ^2_{gca}	.0530	.0148	.0130	59 x 10 ⁻³	81 x 10 ⁻³	14 x 10 ⁻⁴
σ^2_{Error}	.0177	.0321	.0438	16 x 10 ⁻²	21 x 10 ⁻²	21 x 10 ⁻⁴
h^2	.806	.477	.372	.428	.380	.562

Table 12. Combining ability components of variance and narrow sense heritability for six quantitative traits for the combined locations.

	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
$\sigma^2_{g \times 1}$	.0063	.0061	.0114	19×10^{-3}	72×10^{-3}	30×10^{-6}
σ^2_{sca}	.0020	-.0159	.0032	-34×10^{-3}	-43×10^{-3}	19×10^{-5}
σ^2_{gca}	.0682	.0378	.0020	10×10^{-2}	29×10^{-3}	11×10^{-4}
σ^2_{Error}	.0220	.1394	.1360	26×10^{-2}	36×10^{-2}	15×10^{-4}
h^2	.875	.499	.04	.573	.184	.703
			.309*		.647*	

* h^2 values for $\sigma^2_{gca} + \sigma^2_{g \times 1}$ together.

Table 13. GCA effects and variances for six quantitative traits - and ranking by means and GCA effects for parental Groups.

GROUPS	LOC-1			LOC-2			COMBINED					
	gi	σ^2_{gi}	Ranking*	gi	σ^2_{gi}	Ranking*	gi	σ^2_{gi}	Ranking*			
			$\bar{X}$ gi			$\bar{X}$ gi			$\bar{X}$ gi			
AH												
a) T. Tuber Wt.	-.26	.059	4	4	-.20	.033	4	4	-.20	.032	4	4
b) F. Vine Wt.	1.13	1.172	2	2	.43	.173	2	2	.78	.556	2	2
c) Tuber + Vine	.90	.718	3	4	.32	.086	4	4	.53	.230	4	4
d) Dry Vine	.20	.039	1	1	.08	.006	2	1	.14	.019	1	1
e) Total D.M.	.16	.024	4	4	.04	.001	4	4	.10	.009	4	4
TH												
a) T. Tuber Wt.	.72	.510	1	1	.57	.318	1	1	.62	.376	1	1
b) F. Vine Wt.	.61	.267	4	4	.04	-.010	4	4	.32	.050	4	4
c) Tuber + Vine	1.34	1.704	2	3	.67	.432	2	2	1.01	.969	3	3
d) Dry Vine	.04	.000	4	4	.03	.001	4	4	.04	.001	4	4
e) Total D.M.	.17	.027	3	3	.14	.019	2	2	.15	.021	3	3

(cont.)

(cont.)

Table 13. (cont.)

GROUPS	LOC-1			LOC-2			COMBINED		
	gi	σ^2_{gi}	Ranking*	gi	σ^2_{gi}	Ranking*	gi	σ^2_{gi}	Ranking*
			$\bar{X}$ gi			$\bar{X}$ gi			$\bar{X}$ gi
STN									
a) T. Tuber Wt.	.41	.160	2	2	.35	.116	2	.38	.136
b) F. Vine Wt.	.95	.798	3	3	.37	.125	3	.66	.384
c) Tuber + Vine	1.35	1.731	4	2	1.09	1.172	1	1.03	1.010
d) Dry Vine	.13	.016	3	3	.07	.005	3	.10	.009
e) Total D.M.	.20	.039	1	1	.14	.019	1	.16	.024
PHU									
a) T. Tuber Wt.	.25	.054	3	3	.24	.051	3	.28	.070
b) F. Vine Wt.	1.18	1.287	1	1	.48	.218	1	.83	.637
c) Tuber + Vine	1.41	1.896	1	1	.65	.406	3	1.03	1.010
d) Dry Vine	.16	.024	2	2	.09	.008	1	.12	.013
e) Total D.M.	.20	.035	2	2	.13	.016	3	.16	.024

* $\bar{X}$ = mean yield performance of Groups
gi = GCA effects

relatively higher than σ_{gca}^2 without taking into account $\sigma_{gca}^2 \times \text{loc.}$ Regardless of its value, σ_{sca}^2 was relatively small to suggest non-additive type of gene action.

In the present study, it has been also demonstrated that the ranking pattern of the mean yields of the parental Groups, remained unaltered when it was compared to the ranking on the basis of GCA effects which was calculated following certain assumptions (Griffing, 1956). The close agreement of these results indicate that suitable combiners may be selected on the basis of their mean yield performances, making it perhaps unnecessary to estimate GCA effects as is generally done in diallel analysis.

GENERAL DISCUSSION

It was not intended to study strictly the heterosis of the potato Group-hybrids, as has been done with corn synthetics and open-pollinated varieties (Robinson et al., 1956; Lonnquist and Gardner (1961), neither was it intended to make hybrid diploid potato populations to be released as potential varieties. It was intended to gain some insight on the hybrid behavior of haploids and diploids particularly that of Group Andigena, whose parental tetraploid population is well known for its wide genetic diversity. The major problems associated with the use of Gp. Andigena, and which has kept breeders from using it, has been the negative tuberization response under long daylengths and high temperatures, and the lateness transmitted to the progeny. Haploids from this Group inherited the same poor characteristics of their parents to the extent that most of those from the early extractions were lost. Until

haploids are isolated from adapted Gp. Andigena clones, there will be a need to find alternative ways to maintain and use haploids from unadapted parental introductions. To get them in a hybrid haploid-diploid or haploid-haploid populations seem to be a good alternative. The inbreeding depression suffered by haploids after their extraction will be counterbalanced by crossing them with other Groups. These hybrid populations well may be the base population, with a great deal of genetic input from the Andigena Group, to start selection for tuberization under long days or simply to facilitate their clonal maintenance in a hybrid form to be used in genetic or breeding studies. It can also be a source of hybrid clones to be screened for diplandroids and diplogynoids for further polyploidization studies.

The nature of the parental Groups and the Group-hybrid populations, by the way they were formed, suggests their approximation of that of diploid open-pollinated varieties, and they represent a random sample of their respective natural Group parental populations. The analysis of a diallel of cultivars and related populations is of course not new. Several people used it with slight modifications to fit their own requirements (Gardner and Eberhart, 1966; Griffing, 1956; Hayman, 1954; Lonnquist and Gardner, 1961), with the following assumptions: random mating varieties, arbitrary gene frequencies at all loci, diploid inheritance, two alleles per locus and no epistasis.

Results of the combining ability analysis of variance, in the present study, indicated that the additive gene effects of the Groups were important in determining yield crosses. This was to be expected

considering the heterogeneous nature of these Groups which were not subject to any selection for yield previously.

Perhaps, one wonders why we need diploid Group-hybrid populations in a breeding program? The answer is simple, we do not need inter-Group hybrids for direct breeding approach, but it is advisable to build diploid stocks or inter-Group hybrid populations to make use of the cultivated germplasm collection available. The creation of new populations, on which selection for desirable traits can be effectively applied, are more likely to be used by breeding programs. The desirability of these newly generated populations will easily attract breeders and enhance their use in the development of new cultivars.

The understanding of the heterotic behavior of the Group hybrids as well as their breeding behavior and the nature of gene action of desirable quantitative traits will help in moulding cultivated germplasm into more workable forms.

GENETIC VARIATION IN SOLANUM TUBEROSUM GP. ANDIGENA HAPLOIDS

INTRODUCTION

The availability of haploids from tetraploid clones of Solanum tuberosum Groups Tuberosum and Andigena makes possible the study of quantitative genetic variation among them, which is facilitated by their disomic inheritance. The quantification of genetic variation and gene action will undoubtedly help in the understanding and selection of breeding schemes to fully exploit their potential with certainty and effectiveness. Little is known about quantitative variation at the diploid level of Gp. Andigena, but some studies have been done with Gp. Tuberosum haploids (Mendiburu, 1971; Rowe, 1969). In both studies Gp. Tuberosum haploid - Gp. Phureja hybrids were used, and Rowe also used haploids from Gp. Tuberosum. Design I and II (Comstock and Robinson, 1948) were used by Rowe. In both experiments, additive genetic variance was higher than dominant variance for total tuber number and total tuber weight, with one exception when using Design I on inter-haploid-diploid hybrids where dominant variance was greater than additive variance. Mendiburu, using a diallel experiment also found significant general combining ability in separate locations but not in the combined locations analysis. Other than these two attempts to quantify genetic variation at the diploid level in potato, none has been reported. Even less has been done particularly with haploids from Gp. Andigena. Since our interest is to promote the use of Gp. Andigena haploids as a genetic source in breeding, the main objectives in this study were to quantify

their genetic variation for quantitative traits and their heritabilities.
To this end, two different approaches were used.

MATERIALS AND METHODS

The experimental material for this study was produced following a mating scheme described by Comstock and Robinson (1952) as Design I. A random sample of haploids derived from 28 parental introductions of Group Andigena were used as the females. They were crossed in sets to three male Groups composed of Gp. Andigena haploid (AH), Gp. Phureja (PHU) and Gp. Stenotomum (STN). These three male Groups were constituted separately by bulking pollen collected from an equal number of flowers per clone within each group. The progenies within each male group comprised the source material to be evaluated in two separate locations. The female haploid clones used to generate the progenies were also evaluated in adjacent plots in both locations.

Seed germination, seedling handling and transplanting were carried out in parallel and the same way as that described in "Materials and Methods" of the diallel experiment.

The experimental design used to evaluate the progenies and female clones was a randomized complete block, with three replications. The progeny plots were composed of 40 individuals per replication, spaced one foot apart with four feet between rows at Sturgeon Bay and three feet at Hancock. The female clonal plots consisted of five tubers per replication. The transplanting of progenies and female clones to the field was done on June 6 at Hancock and June 12, 1978 at Sturgeon Bay. The harvesting was done during the week of September 27th at Hancock and October 18th at Sturgeon Bay.

Data were obtained on a plot basis and later transformed to plot means. The same six traits described earlier in "Materials and Methods" of the diallel experiment were considered. These are: total tuber weight, fresh vine weight, pooled tuber + vine weight, dry vine weight, total dry matter weight and specific gravity.

The analysis of variance for the progenies was carried out according to Design I (Comstock and Robinson, 1948, 1952). A computer program was used to perform the analysis for each location and the combined locations. Genotypes and locations were considered as random effects. The expectation of mean squares (EMS), and the components of variance were obtained following the standard procedures outlined in Design I (Tables 1, 2). The variance component of males (σ_M^2), which is due to half-sib groups being different among paternal plants, equals the covariance of half-sibs. This estimate is equivalent to one-fourth of the additive genetic variance (σ_A^2). The variance component of females (σ_F^2) estimates one-fourth of the additive genetic variance (σ_A^2) and one-fourth of the dominant genetic variance (σ_D^2).

A second method to estimate heritabilities was performed using data from both the parental clones and the progenies. This model originally described by Lush (1940), also explained in detail by Falconer (1972), and Becker (1967), is called the "intra sire regression of offspring on dam". The covariance of progeny and female parents will estimate one-half of the additive genetic variance (σ_A^2). Dividing the covariance of offspring and female parents by the variance of females, within males, the regression coefficient is obtained.

Twice the regression coefficient will estimate heritability (Becker, 1967). A computer program was also used to perform these calculations.

Table 1. Expected mean squares (EMS), model to estimate component of variances for single locations.

Source of Variation	D.F.	M.S.	E.M.S.
Replications	$(r - 1)$		
Males	$(m - 1)$	M_1	$\sigma_W^2 + K_1 \sigma_F^2 + K_2 \sigma_M^2$
Females in Males	$m(f - 1)$	M_2	$\sigma_W^2 + K_1 \sigma_F^2$
Females/Males x Rep.	$mf(r - 1)$	M_3	σ_W^2

K_1 = number of plots/maternal line
 K_2 = number of plots/paternal line (harmonic mean is used because of unequal number of females within males)

Table 2. Expected mean squares (EMS), model to estimate component of variances for the combined locations.

Source of Variation	D.F.	M.S.	E.M.S.
Locations	(1 - 1)		
Males	(m - 1)	M_1	$\sigma_W^2 + K_1 \sigma_F^2 \times L + K_1 l \sigma_F^2 + K_2 \sigma_M^2 \times L + K_2 l \sigma_M^2$
Females/Males	m(f - 1)	M_2	$\sigma_W^2 + K_1 \sigma_F^2 \times L + K_1 l \sigma_F^2$
Males x Loc.	(m - 1)(1 - 1)	M_3	$\sigma_W^2 + K_1 \sigma_F^2 \times L + K_2 \sigma_M^2 \times L$
Females/Males x Loc.	m(f - 1)(1 - 1)	M_4	$\sigma_W^2 + K_1 \sigma_F^2 \times L$
Error	mf1(r - 1)	M_5	σ_W^2

K_1 = number of plots/maternal line

K_2 = number of plots/paternal line (harmonic mean is used because of unequal number of females within males)

RESULTS

The analyses of variance for all traits over all locations is presented in Tables 3, 4 and 5. Tests for homogeneity of variances were performed according to the appropriate F ratio suggested by the expected mean squares (EMS). For each location the degrees of freedom used to obtain the tabulated F values of the sources of variations, were those of their respective sources. However, for the combined analysis, where the expected mean squares (EMS) indicated the use of more than two main sources to test "Males" mean squares, the degrees of freedom to obtain F tabulated were obtained following the scheme suggested by Cochran and Cox (1957). The mean square of males at location 1 (Table 3), were significant for total tuber, vine, dry vine and specific gravity. Although tuber + vine and total dry matter mean squares were not significant, they were higher than the remaining sources. The amount of additive genetic variances, obtained out of the male source of variation for these traits, agrees quite well with the mean squares. At location 2 (Table 4), total tuber and dry vine were statistically significant in the analysis of male source of mean squares. The remaining traits, although reasonably high were not significant. In the combined analysis (Table 5), the mean squares of males were not significant for all traits, but their amount is relatively high compared to the mean squares of other sources of variation except for locations. Locations were significant and the interaction of males x locations had significant mean squares for total tuber, vine,

Table 3. Analysis of variance for six quantitative traits (location 1, Sturgeon Bay).

Source of Variation	D.F.	MEAN SQUARES (M.S.)					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
Males	2	.5076*	8.2976*	5.8945	.1482*	.1227	6361 x 10 ⁻³
Females/M ₁	3	.0085	2.5885**	2.4334**	.0425**	.0360*	3805 x 10 ⁻³
Females/M ₂	9	.0354	1.0679**	1.0785*	.0249*	.0262*	733 x 10 ⁻⁴
Females/M ₃	6	.0055	2.7232**	2.8625**	.0524**	.0480**	7107 x 10 ⁻⁴
Error	41	.0201	.2984	.2905	.0088	.0094	6367 x 10 ⁻⁴
Mean		.3506	3.8394	4.1999	.5489	.6073	1.063
% C.V.		40.4	14.2	12.8	17.1	15.9	.7

* significant at 5%

** significant at 1%

M₁, M₂, M₃ = AH, PHU and STN male parents, respectively.

Table 4. Analysis of variance for six quantitative traits (location 2, Hancock).

Source of Variation	D.F.	MEAN SQUARES (M.S.)					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
Males	2	.2507**	.4987	.3522	.0192*	.0084	1292×10^{-3}
Females/M ₁	5	.0278	.3472**	.3750**	.0072	.0069	4969×10^{-4}
Females/M ₂	10	.0225	.2515**	.3323**	.0133*	.0175**	1144×10^{-3}
Females/M ₃	6	.0340*	.2383*	.1530**	.0084	.0096	2976×10^{-4}
Error	47	.0118	.0761	.0947	.0053	.0058	3586×10^{-4}
Mean		.5072	1.4439	1.9534	.3137	.4015	1.069
% C.V.		21.4	19.1	15.8	23.2	18.9	.5

* significant at 5%

** significant at 1%

M₁, M₂, M₃ = AH, PHU and STN male parents, respectively.

Table 5. Analysis of variance for six quantitative traits. Combined locations.

Source of Variation	D.F.	MEAN SQUARES (M.S.)					
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
Locations	1	.8800**	141.7091**	120.2177**	1.2642**	.8946**	$106 \times 10^{**}$ -2
Males	2	.5731	7.0280	4.6240	.1459	.1105	553×10 -3
Females/M ₁	3	.0295*	2.5930	2.3342	.0456	.0360	302×10 -3
Females/M ₂	9	.0422	1.0044*	1.0699*	.0264*	.0279	$176 \times 10^{**}$ -3
Females/M ₃	6	.0241	2.2620	2.0467	.0490	.0475*	708×10 -4
Males x Loc.	2	.0755*	2.1464*	1.7125	.0316*	.0293	$216 \times 10^{*}$ -3
Fem. x Loc./M ₁	3	.0018	.4672	.4836	.0065	.0072	134×10 -3
Fem. x Loc./M ₂	9	.0161	.2361	.2433	.0078	.0112	221×10 -4

Table 5. (cont.)

Source of Variation	D.F.	MEAN SQUARES (M.S.)				
		Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter
Fem. x Loc./M ₃	6	.0151	.7013**	.9712**	.0119	.0101
Error	83	.0162	.1824	.1881	.0072	.0077
Mean		.4409	2.6438	3.0938	.4319	.5072
% C.V.		28.9	16.2	14.0	19.6	17.3

* significant 5%

** significant 1%

M₁, M₂, M₃ = AH, PHU and STN male parents, respectively.

⁻⁴
303 x 10

⁻⁴
511 x 10

1.006

.6

dry vine and specific gravity. The interaction of females x locations within male 3 (STN), was also significant for vine and tuber + vine.

The estimates of components of variance and heritability, for both individual locations and the combined, are presented in Tables 6, 7 and 8. At location 1, the heritability for tuber yield was rather high compared to the other traits (Table 6), although these other traits were within the expected range for polygenic traits. Heritabilities at location 2, for all traits except total tuber, were considerably lower than those at location 1 (Table 7). Fresh vine was 22.4%, the pooled tuber + vine was very low (6.3%), dry vine 18.6%, the total dry matter fell down to zero and specific gravity became unusually low (16.4%). These differences may indicate a differential behavior of the genotypes under different environments. However, the amount of the error components of variance (σ_E^2) within location 2 had increased a great deal compared to the genetic components of variance (σ_M^2 or σ_F^2).

The estimates of components of variance for the combined locations (Table 8), partially answers the effect of the environment on the genotypes and their interaction effects on the estimates of heritabilities. The $\sigma_{M \times \text{loc.}}^2$ component for total tuber, in proportion to σ_M^2 , is several times lower than those of the other traits. This indicates that the effect of the interaction, genotype x environment, for total tuber yield is low, consequently the true heritability for this trait remains high. The remaining traits had higher $\sigma_{M \times \text{loc.}}^2$ component, making up to about 50% of the main genetic source of variation; therefore, biasing the estimates of the additive genetic variance.

Table 6. Design I components of variance and narrow sense heritability (location 1, Sturgeon Bay).

Variances	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_M^2	.0266	.3516	.1639	.0061	.0048	2804×10^{-4}
σ_F^2	.0003	.5249	.5361	.0094	.0086	2003×10^{-4}
σ_E^2	.0201	.2984	.2905	.0088	.0094	6367×10^{-4}
σ_T^2	.1268	2.2297	1.4822	.0425	.0372	1958×10^{-3}
h^2	.839	.631	.442	.573	.516	.573

Table 7. Design I components of variance and narrow sense heritability (location 2, Hancock).

Variances	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_M^2	.0100	.0102	.0027	.0004	-.0002	24×10^{-5}
σ_F^2	.0051	.0648	.0655	.0017	.0023	129×10^{-4}
σ_E^2	.0118	.0761	.0947	.0053	.0058	359×10^{-4}
σ_T^2	.0569	.1817	.1710	.0086	.0150	585×10^{-4}
h^2	.702	.224	.063	.186	.000	.164

Table 8. Design I components of variance and narrow sense heritability. Combined locations.

Variances	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_M^2	.0131	.0991	.0501	.0024	.0015	59×10^{-5}
σ_F^2	.0034	.2098	.1800	.0047	.0043	20×10^{-4}
$\sigma_M \times 1$	.0034	.0939	.0649	.0012	.0010	95×10^{-5}
$\sigma_F \times 1$	-.0009	.0824	.1127	.0006	.0008	-26×10^{-5}
σ_e^2	.0162	.1824	.1881	.0072	.0077	51×10^{-4}
σ_T^2	.0707	1.2471	.6607	.0268	.0167	88×10^{-4}
h^2	.741	.318	.303	.352	.359	.270

However, this was not the only component affecting heritability. If we examine the error component of variance for all traits (Table 8), all but tuber yield had relatively high values. Since these components (σ_E^2) are part of the non-genetic variance of the total Phenotypic variance (σ_P^2), the ratio σ_A^2/σ_P^2 were lowered.

Heritability estimates using parent-offspring regression analysis were calculated for all traits except specific gravity. These values indicated a reasonable amount of heritability existed for both locations and the combined locations (Table 9). However, heritabilities at location 2, for all traits with the exception of tuber yield were lower than those at location 1, as was also observed in the Design I analysis. The standard errors at location 2 were also slightly higher than those at location 1. In the combined analysis, all traits had heritabilities ranging in between the two locations, but the standard errors were lower.

The genetic variance, additive (σ_A^2) and dominant (σ_D^2), were estimated for each location and the combined locations (Tables 10, 11, 12). According to the symbolism of Comstock and Robinson (1948), the variances of males (σ_M^2), is equal to one-fourth of σ_A^2 , and the variance of females (σ_F^2), is equal to one-fourth of σ_A^2 and one-fourth of σ_D^2 . Thus $\sigma_A^2 = 4\sigma_M^2$ and $\sigma_D^2 = 4(\sigma_F^2 - \sigma_M^2)$.

The additive genetic variance for total tuber yield in this study, for each location and the combined, was higher than σ_D^2 (Tables 10, 11, 12). In fact σ_D^2 was negative. However, since variances by definition are never negative, it is most reasonable to conclude that the true values of these negative variances resulted from sampling error

Table 9. Heritability estimates, using intra-sire regression of offspring on female for two locations and the combined.

TRAITS	LOCATION 1		LOCATION 2		COMBINED	
	h^2	S.E.	h^2	S.E.	h^2	S.E.
Total tuber wt.	.228	.132	.457	.188	.338	.115
Fresh vine wt.	.544	.153	.319	.172	.515	.106
Tuber + vine wt.	.560	.160	.390	.170	.523	.110
Dry vine wt.	.532	.137	.235	.138	.416	.098
Total dry matter wt.	.468	.142	.244	.157	.374	.105

S.E. = standard error

(Robinson et al, 1955). Other traits such as vine, dry vine, total dry matter and specific gravity, at location 1 (Table 10), also had higher σ_A^2 than σ_D^2 . The pooled tuber + vine weight, at this same location, had lower σ_A^2 than σ_D^2 . At location 2 (Table 11), all traits but total tuber weight had higher σ_D^2 than σ_A^2 . In the combined analysis (Table 12), most traits but total tuber and dry vine had higher σ_D^2 than σ_A^2 , but not as great as at location 2 in proportion to σ_A^2 . These results suggest that σ_A^2 is mainly important for tuber yield. On the other hand, both σ_A^2 and σ_D^2 are relatively important in the remaining traits within this particular population. Moreover, if we examine the genetic coefficients of variation (Tables 10, 11, 12), they ranged from 24.9 to 93.0 percent. A coefficient of 20 percent indicates a range in genetic value for roughly 50 to 150 percent of the mean of the character (Comstock et al, 1957), an amount of variation that can not be viewed as small. According to this criterion, the estimate of the total genetic variance was large for each of the six characters in each location and the combined.

Table 10. Genetic variances, genetic coefficient of variation (G.C.V.) and means (location 1, Sturgeon Bay).

Genetic Component	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_A^2	.1064	1.4064	.6556	.0244	.0192	112×10^{-3}
σ_D^2	-.1052	.6932	1.4888	.0132	.0152	-32×10^{-4}
G.C.V.	93.0	37.7	34.8	35.3	30.5	31.4
Mean	.351	3.840	4.200	.549	.607	1.063

Table 11. Genetic variances, genetic coefficient of variation (G.C.V.) and means (location 2, Hancock).

Genetic Component	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_A^2	.0400	.0408	.0108	.0016	-.0004	96×10^{-5}
σ_D^2	-.0196	.2184	.2512	.0052	.0100	42×10^{-4}
G.C.V.	39.4	35.2	26.2	26.2	24.9	67.1
Mean	.507	1.444	1.953	.314	.402	1.069

$$\text{Genetic C.V.} = \frac{\sqrt{\sigma_A^2 + \sigma_D^2}}{\text{Mean}} \times 100$$

Table 12. Genetic variances, genetic coefficient of variation (G.C.V.) and means. Combined locations.

Genetic Component	Total Tuber Wt.	Fresh Vine Wt.	Tuber + Vine	Dry Vine	Total Dry Matter	Specific Gravity
σ_A^2	.0524	.3964	.2004	.0096	.0060	24×10^{-4}
σ_D^2	-.0388	.4428	.5196	.0094	.0112	56×10^{-4}
G.C.V.	51.9	31.7	27.4	28.5	25.8	83.9
Mean	.441	2.644	3.094	.432	.507	1.066

$$\text{Genetic C.V.} = \sqrt{\frac{\sigma_A^2 + \sigma_D^2}{\text{Mean}}} \times 100$$

DISCUSSION

The analysis of variance of the mating scheme followed (Design I); the estimates of components of variance, and their interpretation genetically by translating them into covariances of relatives, were based on the assumptions proposed elsewhere (Comstock and Robinson, 1948, 1952; Cockerham, 1956). The narrow sense heritabilities obtained for all traits indicated the relative importance of the additive fraction of the total genetic variance. Its amount will determine the rate of progress if selection were to be done for that character in that population. Although total tuber yield heritability was relatively high, the remaining traits have essentially moderate heritability values, perhaps with the exception of those at location 2, where heritabilities were rather low. Examining the combined analysis (Table 8), the interaction "males x location" components of variance ($\sigma_{M \times loc.}^2$), for most traits, except total tuber and dry vine, were relatively comparable to the amount of the male component of variance (σ_M^2). This may indicate that there is an effect of genotype x environment interaction on the additive genetic variance, consequently on heritability. Several authors have shown the same effects (Comstock, 1955; Comstock and Robinson, 1952; Le Roy, 1960; Rojas and Sprague, 1952). Other components, such as the error variance (σ_E^2), which was relatively high, may have also reduced the heritability values. Sampling errors may be high, even when considerable data is investigated, particularly for low heritable traits (Cockerham, 1956).

Estimates of heritability from parent-offspring regression analysis (Table 9) at location 1 were reasonably close to that obtained with Design I for most traits, except tuber yield that had a rather low value with the parent-offspring regression and a high value by Design I. These estimates at location 2, apart from tuber yield, were higher than those obtained using Design I. In the combined location analysis, the heritability estimates from the parent-offspring regression for dry vine and total dry matter were reasonably close to those obtained with Design I; but the tuber yield estimate was lower and fresh vine, pooled tuber + vine estimates were higher than those obtained with Design I. In general these heritability values were highest at location 1, lowest at location 2 and intermediate in the combined for both Design I and parent-offspring regression analysis. Robinson et al (1949), working with F_2 corn populations from single hybrids, obtained estimates of heritability using both methods, Design I and regression of offspring on female and male parents. He found discrepancies among heritability estimates within each hybrid for certain characters. He refers to them as being not unexpected; occasionally unexplainable discrepancies should occur among the three estimates for a single character. However, when heritabilities were obtained from all hybrids, the agreement was reasonable. In the present study, these discrepancies could have also been due to results of sampling error; however, genuine differences between these two methods may have also contributed to it. The standard errors in the parent-offspring heritabilities were in general quite high.

Becker (1967), argues that this is because of the small number of males and females used. This was true in the present instance, particularly for males.

The total amount of genetic variation estimated with Design I, which assumes no epistasis (Tables 10, 11, 12), appears to be high (Comstock et al, 1957; Rowe, 1969), based on the genetic coefficients of variation for all traits over all locations. Both additive and dominant genetic variances are present in all traits with the exception of tuber yield where the additive genetic variance is more important. Whether, additive or both additive and dominant genetic variances are needed to describe the genetic variance observed, an efficient population breeding method to meet either requirement can be easily applied.

Fertility and 2n Gamete Frequency in Hybrid Families

From AH, TH, STN and PHU Crosses

INTRODUCTION

Several wild diploid species from different taxonomic Series of the tuber-bearing Solanums, as well as cultivated diploids including Solanum tuberosum Groups Phureja, Stenotomum, Tuberosum haploids and hybrids among diploid-Tuberosum haploids, were subject to screening for 2n gametes (Den Nijs and Peloquin, 1977; Hanneman and Peloquin 1967; Quinn et al, 1974). Results were variable, but indicated the presence of both diplandroids and diplogynoids. Hanneman and Peloquin (1967) reported, from crosses of 24-chromosome hybrids (2x) with 48-chromosome cultivars (4x), averages of 2.10 seeds/fruit for the 2x x 4x cross, and 1.76 seeds/fruit for 4x x 2x crosses. Aside from these average figures, variability for seed set among clones was observed. Three of the 24-chromosome hybrid clones stood out, averaging more than 20 seeds/fruit when crossed as males to tetraploid cultivars. Several of these clones after subsequent studies proved to produce 2n pollen by first division meiotic restitution (FDR) due to parallel spindles at anaphase II (Mok et al, 1975). Quinn et al (1974), did extensive screening for diplandroids among 34 diploid species involving five taxonomic Series. Seven of them produced five percent or more 2n pollen. Pollen size from species-haploid hybrids was used to discriminate between 2n and n pollen, and the frequency was correlated to seed set following 4x x 2x crosses. They found a high correlation between 2n pollen and seed set. Den Nijs and Peloquin (1977), also screened for diplandroids and diplogynoids in ten

species. Eight species tested for 2n egg production proved to have at least two PI's within each species in which some clones formed 2n eggs following 2x x 4x crosses. The screening for 2n pollen producing clones was done on 25 species involving seven different Series. They reported that the overall number of clones that produced 2n pollen was low and the percentage of 2n pollen observed was low as well, but sufficient to provide evidence of 2n pollen.

The widespread occurrence of diploids capable of producing 2n gametes and the concurrent demonstration that such 2n gamete producers hybridize well with tetraploid cultivars (Hanneman and Peloquin, 1968; Mendiburu and Peloquin, 1977; Quinn and Peloquin, 1973), provide evidence of the possibility of identifying 2n gamete producing clones for cytogenetic, genetic and breeding studies. Since these possibilities also include the present material under investigation, the objectives were, first to assess the fertility of the hybrid populations and second, to determine the frequency of 2n gametes in these populations as a complement to the integral study of Gp. Andigena haploids and their hybrids.

MATERIALS AND METHODS

The progenies of the Group-hybrid families were described in an earlier section (Diallel experiment). They were used to determine both fertility (male and female), and presence of $2n$ gametes in the present section. Male fertility was scored by observation of pollen shedding of every plant within each family in two locations - Sturgeon Bay and Hancock. A second criterion was also used to test male fertility, and this was related to pollen stainability. Equal numbers of flowers from individuals within each family were collected and bulk pollen was collected. The pollen was stained with aceto-carmin and the stainability scored.

Female fertility was measured by the amount of seed set from a random sample of open-pollinated fruit. These fruit were collected directly in the field from the sampled plants within each family by picking one seedball per plant.

The presence of $2n$ gametes (diplandroids and diplogynoids), in each family was determined in the following manner: diplandroids were scored according to the frequency of stainable large pollen which had a diameter of 30 microns or more compared to n pollen which usually had a smaller diameter ($\pm$ 25 microns). A second method to estimate diplandroids was based on the amount of seed set per fruit following $4x \times 2x$ crosses. To determine the presence of $2n$ eggs, a sample of clones within families were crossed as females to a tetraploid source of pollen (cultivars). The amount of seed set per fruit indicated the presence of $2n$ eggs in that particular family.

RESULTS

Male and female fertility.

Pollen shedding and stainability results are presented in Table 1. It is noticeable that more than 95% of the total individuals within families, including Gp. Andigena haploids (AH), Gp. Phureja (PHU), Gp. Stenotomum (STN), hybrids among them and reciprocals, shed pollen; and the stainability of their bulk pollen was in the range of 50 to 70 percent, with the exception of the STN family which had 40-50 percent stainable pollen. In contrast, the hybrid families among Gp. Tuberosum haploids with AH, PHU and STN had 5% or less of individuals shedding pollen (Table 1), and their pollen stainability was relatively low (20-40%). This was not surprising, because of the well-known interaction of TH cytoplasm with genes of the cultivated diploid species conditioning male sterility (Hougas and Peloquin, 1962). Reciprocal crosses of TH x STN and TH x PHU were not attempted because of the high degree of male sterility of the TH source (Peloquin and Hougas, 1960).

Female fertility of the segregant families was assessed based on seed set per fruit from a random sample of open-pollinated fruit (Table 2). A relatively high seed set was obtained for AH x AH, PHU and STN; likewise for progenies from AH x STN, AH x PHU and reciprocal hybrids. Some reciprocal differences were observed for seed set among these hybrids. Apparently with STN and PHU (cytoplasm), seed set was higher; however, no conclusive statements could be made from these observations due to the uncontrolled nature of the pollinations. F_1

Table 1. Male fertility as measured by pollen shedding and pollen stainability of AH, PHU, STN and TH hybrid families and of PHU and STN bulk populations.

Families	Clones			Percent Shedding	Stainable Pollen (%)
	Total	# Shedding	# Not Shedding		
AH x AH	343	337	6	98	50-60
AH x PHU	348	330	18	95	50-60
PHU x AH	336	336	0	100	60-70
AH x STN	348	341	7	98	50-60
STN x AH	343	343	0	100	60-70
TH x AH	342	18	324	5	20-30
TH x STN	350	18	332	5	20-30
TH x PHU	344	11	333	3	30-40
STN	273	273	0	100	40-50
PHU	332	332	0	100	50-60

Table 2. Female fertility as measured by seed set from a random sample of open-pollinated fruit of AH, PHU, STN and TH hybrid families and PHU and STN bulk populations.

Families	No. of Fruits	Total No. Seeds	No. Seeds/Fruit
AH x PHU	32	2982	93.2
PHU x AH	26	4049	155.7
AH x STN	65	4643	71.4
STN x AH	37	6360	171.8
TH x AH	0	-	-
TH x STN	4	667	166.8
TH x PHU	3	373	124.3
AH x AH	25	3886	155.4
STN	30	2372	79.1
PHU	34	4224	124.2

families from TH x AH, TH x STN and TH x PHU hybrids, which were previously demonstrated to have relatively high female fertility (Hougas and Peloquin, 1960; Ross, Peloquin and Hougas, 1964), almost failed to set open-pollinated fruit (Table 2). Besides, pollen shedding of these hybrids was almost nil (Table 1). Perhaps, because of the lack of pollen, insect pollinators were not attracted to the flowers; consequently, pollination did not take place among these individuals and fruit set failed. However, four and three fruits from TH x STN and TH x PHU progenies, respectively, were collected, and they averaged 166.8 and 124.3 seeds/fruit, respectively. No fruit were found among individuals from TH x AH hybrid.

Presence of 2n gametes.

Bulk pollen from the hybrid families AH x AH, AH x STN and AH x PHU was used in 4x x 2x crosses to determine the frequency of 2n pollen in each population. Seed set per fruit was the criterion used to determine the functioning of 2n pollen since virtually all of the seed was expected to be tetraploid. The effective triploid block operating in inter-ploidy crosses of this kind eliminates almost all triploid embryos due to endosperm imbalance (Hanneman and Peloquin, 1967; Marks, 1966; von Wangenheim et al, 1960). Hybrids TH x AH, TH x STN and TH x PHU were not used because of their male sterility. The average seed set per fruit of five tetraploid cultivars pollinated with AH x AH, AH x STN and AH x PHU hybrids is presented in Table 3. AH x AH crossed onto Kennebec had the highest average seed set (7.3 seeds/fruit); however, the mean over all varieties was 5.1 seeds/fruit. AH x STN had its

Table 3. Presence of 2n pollen in AH x AH, AH x STN and AH x PHU diploid hybrid families measured by seed set after crossing to tetraploid cultivars (4X x 2X).

4X x 2X Crosses	No. Pollinations	No. Fruits	No. Seeds	No. Seeds/Fruit
Sebago x (AH x AH)	21	3	1	.3
Ontario x (")	20	3	6	2.0
Katahdin x (")	17	9	34	3.7
Red Pontiac x (")	18	13	51	3.9
Kennebec x (")	40	24	175	7.3
Total	216	52	267	5.1
Sebago x (AH x STN)	52	22	11	.5
Ontario x (")	42	9	26	2.9
Katahdin x (")	44	27	39	1.4
Red Pontiac x (")	43	33	46	1.4
Kennebec x (")	44	26	60	2.3
Total	225	117	182	1.6
Sebago x (AH x PHU)	39	11	9	.8
Ontario x (")	55	11	25	2.3
Katahdin x (")	41	28	34	1.2
Red Pontiac x (")	47	37	62	1.7
Kennebec x (")	39	21	71	3.4
Total	221	108	201	1.9

highest seed set when crossed to Ontario (2.9 seeds/fruit), but the over all mean was 1.6 seeds/fruit. AH x PHU had an average of 1.9 seeds/fruit over the five cultivars; however, the highest seed set was on Kennebec (3.4 seeds/fruit).

Prior to the 4x x 2x crosses, the occurrence of 2n pollen was recorded for the hybrid families as well as PHU and STN, based on the size of stainable pollen (Table 4). Most of the families had less than one percent large stainable pollen; however AH x AH, TH x AH, TH x PHU and TH x TH had from 1 to 5% large pollen. The total pollen stainability, on which the percent of 2n pollen was based on was relatively high for most families, except for TH x AH, TH x STN, TH x PHU, and TH x TH where it was relatively low. Families AH x STN and AH x PHU and their reciprocals did not differ in frequency of 2n pollen; therefore, these reciprocals were not treated separately. Stainability and 2n pollen from TH x AH, TH x STN and TH x PHU, was determined using the scarce pollen obtained; consequently, they were not used as male sources in 4x x 2x crosses. The presence of 2n eggs was confirmed by 2x x 4x crosses. Seed set per fruit was taken as a measure of the 2n eggs potential of a particular family. The average seeds/fruit are presented in Table 5. Most of the families had less than 1.0 seed/fruit with the exception of AH x STN and TH x PHU which averaged 1.7 and 1.8 seeds/fruit respectively. The efficiency of the 2x x 4x cross to determine the total frequency of 2n eggs, as measured by seed/fruit, among sampled clones within families, was greatly reduced by the presence of parthenocarpic fruits; consequently, the average seed set was relatively low. However, variability in the ability to produce

Table 4. Frequency of 2n pollen in AH, PHU, STN and TH hybrid families and PHU and STN bulk populations based on the average stainable large pollen.

Families	Percent of Large Stainable Pollen ($> 30 \mu$.)	Percent of Total Stainable Pollen
AH x AH	1.0-5.0	50-60
AH x PHU	< 1.0	50-60
PHU x AH	< 1.0	60-70
AH x STN	< 1.0	50-60
STN x AH	< 1.0	60-70
TH x AH	1.0-5.0	30-40
TH x STN	< 1.0	20-30
TH x PHU	1.0-5.0	30-40
TH x TH	1.0-5.0	20-30
STN	< 1.0	40-50
PHU	< 1.0	50-60

Table 5. Presence of 2n eggs among AH, PHU, STN and TH diploid hybrid families as measured by seed set following 2x x 4x crosses.

Crosses	No. Clones	No. Pollinations	No. Fruit	No. Seeds	No. Seeds/Fruit
(AH x AH) x 4x ¹	48	239	18	10	.6
(AH x PHU) x 4x	80	485	81	32	.4
(AH x STN) x 4x	76	455	71	118	1.7
(TH x AH) x 4x	61	303	15	5	.3
(TH x STN) x 4x	57	286	2	0	0
(TH x PHU) x 4x	52	260	5	9	1.8

¹ bulk pollen from cultivars Sebago, Ontario, Katahdin, Red Pontiac, and Kennebec

2n eggs was also observed among clones within families. Several clones were identified as having between 10 to 35 seeds/fruit.

DISCUSSION

Male and female fertility.

Male fertility of the F_1 hybrid families, based on pollen shedding and stainability, was found to be relatively high for the intra AH hybrid family; and similarly for families from crosses between AH with STN and PHU including reciprocals. This agrees with previous reports (Cipar et al, 1964; De la Puente, 1966, 1973), where regardless of the direction of the crosses among AH with STN and PHU, the progenies were male fertile. No plasmon differences among these three groups seems to exist. In contrast, hybrid families obtained from crossing TH with STN and PHU were highly male sterile. Most of the clones did not shed pollen, and the stainability of the pollen collected from these few clones that did shed was low compared to that of the AH hybrids. This goes along with the hypothesis of interaction of TH cytoplasm with genes from AH or the cultivated diploids (Cipar et al, 1964; De la Puente, 1966; Hougas and Peloquin, 1962).

Female fertility was relatively high for all hybrid families including those with TH, as judged by the amount of seed set per fruit from open pollinated fruits. However, the progenies from hybrids of TH with STN or PHU did not set as many fruits as those from AH hybrids. This fact can not be contributed to female sterility. The simple presence of flowers lacking pollen apparently did not have any attraction for pollinator insects and thus, resulted in failure to set fruit. Besides, it was known from crossability tests of raw TH haploids with AH, STN and PHU in the previous section, and other studies of haploid

families (De la Puente, 1966; Perez-Ugalde et al, 1964; Ross et al, 1964; Sosa-Chevez and De Sosa, 1972), that female fertility was reasonably high.

Presence of 2n gametes.

The presence of both 2n pollen and 2n eggs in the hybrid families, expressed by seed set following 4x x 2x or 2x x 4x crosses, was expected. There were previous reports about their presence in clones of the parental Groups (Den Nijs, 1977; Hanneman and Peloquin, 1968; Mok, 1975; Mok and Peloquin, 1975; Quinn et al, 1974; Van Suchtelen, 1966; von Wangenheim et al, 1960). Perhaps the most striking feature was the total amount of seeds obtained following both 4x x 2x and 2x x 4x crosses. These seeds obtained by unilateral sexual polyploidization are expected to be tetraploids (Den Nijs, 1977; Hanneman and Peloquin, 1967; Marks, 1966). The total of 650 seeds from 4x x 2x crosses and 174 from 2x x 4x crosses were readily obtained. Of course chromosome counting needs to be done to provide definitive proof of tetraploid nature of the progeny.

The occurrence of both 2n pollen and 2n eggs in these hybrid sources offers a unique opportunity to identify clones with high 2n gamete frequencies. Besides, once these clones are identified within each hybrid-group combination, the possibility of obtaining tetraploids through bilateral sexual polyploidization (Mendiburu et al, 1974), with different Group genome combinations is undoubtedly great. At least 16 Group genome arrangements can be generated from the present material if both 2n pollen and 2n egg sources are found to be formed by first division meiotic restitution (Table 6).

Table 6. AH, PHU, STN and TH hybrid family sources where 2n pollen and 2n eggs were identified and possible tetraploids that could be formed upon bilateral sexual tetraploidization.

Families	2n Pollen	2n Eggs	Possible Tetraploid ¹ Genome Combinations
AH x AH	+	+	AAAS, AAAP, AAAT,
AH x STN	+	+	AAPT, AAST, AATT, ATSS,
AH x PHU	+	+	AASP, ASTP, ASTT
TH x AH*	+	+	APPT, APTT, ATTT
TH x STN*	+	+	SPTT, STTT, PTTT
TH x PHU**	+	+	
TH x TH	+	+	

Alternatives:

* TH male fertiles can be used on AH or STN to obtained families on which 2n gametes producing clones can be screened

** Already available in other sources (ie US-W 5295.7, US-W 1268.8, US-W 5293.3, US-W 5853.2) (Mok, 1975)

¹ Each letter represents a genome derived from its respective parent
A = Gp. Andigena S = Gp. Stenotomum T = Gp. Tuberosum P = Gp. Phureja

The benefit of intra- and inter-locus interactions transmitted by FDR $2n$ gametes, and effectively used by different genome arrangements in the synthesis of tetraploid genotypes, would give a unique variety of heterotic expressions according to the allelic input provided by the genomes. Theoretically the most diverse type, which would be the genotype having AH, PHU, STN and TH genomes in its constitution, would have the best chances to maximize heterozygosity. If these four genomes effectively maximize heterozygosity at most loci, so that tetrallelic and triallelic genotype structures are predominant; then heterosis will be greatly enhanced by the third and second intra-allelic interactions as a result of the presence of mainly three and four alleles per locus as described by Busbice and Wilsie (1966). However, it would be worthwhile, from the genetic and breeding standpoint, to evaluate other tetraploid genotypes with different levels of genomes in their constitution to best ascertain their breeding values and heterosis.

GENERAL DISCUSSION

The different sections covered in the present study, were carried out to provide answers to the general objective of determining the breeding potential of Gp. Andigena haploids. Extensive crossability studies with a large number of AH clones were done, to determine their crossing behavior with other cultivated diploid and haploid Groups. It was learned that AH rather readily crosses with these diploid sources as indicated by other researchers (Hougas and Peloquin, 1960; De la Puente, 1973; Sosa-Chavez and Hernandez de Sosa, 1972). The male and female fertility of AH was found to be relatively high as judged by the average seed set per fruit as shown in Table 1, Section 1 (crossability). No great reciprocal differences were observed with regard to male fertility when AH was crossed to the cultivated diploids STN and PHU as is usual when TH is crossed to these diploids (Cipar and Peloquin, 1964; De la Puente, 1966; Peloquin and Hougas, 1962). These particular facts permit the exploitation of considerable Gp. Andigena germplasm through haploidy without having the constraint of male sterility exhibited by their haploids nor their hybrids with diploid cultivated relatives. In contrast, haploids from Gp. Tuberosum are mainly male sterile and their hybrids with cultivated diploids are almost completely male sterile, when they provide the cytoplasm, because of the cytoplasm-gene interaction conditioning it. Consequently, there is a limitation on using Gp. Tuberosum haploids in breeding; as a matter of fact, most hybrid diplan-droids (Gp. Phureja x Gp. Tuberosum haploid), presently used to obtain

diplandrotetraploids (DTO's), came from families derived from very few TH male fertile clones used as males on Gp. Phureja clones.

The diversity of male fertile Gp. Andigena haploid clones and hybrids that can be made with the cultivated diploid would be a great advantage in preserving genetic diversity. They would also constitute a broad base for selection for tuberization under long daylengths. Adapted Gp. Andigena clones such as the Neo-tuberosum population, would be tremendously advantageous to use as the parental source of Gp. Andigena haploids, since little or no selection for tuberization under long days would be required and they could be used immediately in breeding.

Heterosis among hybrids of AH with other haploid and diploid Groups (TH, PHU, STN), was not clearly indicated on the population basis, for tuber yield. This could have been due to the nature of the short-daylength reaction for tuberization inherited by the hybrids from the parental AH; consequently, reducing the ability to form tubers under long day conditions. However, it was clearly noticed that tuberization was largely increased in the hybrid families. Simmonds (1960), and Rothacker (1962), reported similar results in crosses between Gp. Andigena and Gp. Tuberosum clones at the tetraploid level, but after a few cycles of selection for tuberization under long daylengths in the Gp. Andigena population, heterosis was detected in crosses to Gp. Tuberosum cultivars. Similarly in the present study when semi-adapted Gps. STN and PHU were crossed to TH, heterosis for tuber yield was demonstrated.

In an effort to detect heterosis in Group hybrids, particularly in AH hybrids, other traits were also taken into account, and Table 6, Section 2 (heterosis and combining ability) indicates that the average AH F_1 mean was five percent higher than the mid-parent for dry vine weight, and 5.9 percent for total dry matter weight, which includes both tubers and vine dry matter. This may in fact suggest that hybrid vigor was expressed by the AH F_1 hybrids; but due to the negative effect of daylength on tuberization, they were not able to demonstrate heterosis for tuber yield.

The combining ability analyses, on a population basis, as indicated in Tables 7, 8, and 9 in Section 2, was highly significant for general combining ability for both tuber yield and specific gravity. The heritability values, were large enough to ensure progress with any selection scheme, taking into account additive genetic variance. This is important because it entails the effective upgrading of the basic chromosome sets in the haploid and diploid populations based on additive gene action, before the synthesis of diploid hybrids takes place; as outlined by Chase (1963) in breeding at the diploid level in his analytic breeding scheme. Besides, selection within the diploid sources should tend to maintain and increase genetic diversity prior to the synthesis of the intermediate diploid hybrids, and between these hybrids, so as to insure the production of two successive rounds of heterosis, as pointed out by Mendiburu et al, (1974).

The genetic variation of the AH population was also investigated on a wide sample of AH clones tested with three parental Group

populations. The Design I, as described by Comstock and Robinson (1948, 1952), was used for this purpose. A Parent-offspring regression analysis was also used to study genetic variation in the same material used in Design I. Once more, the additive genetic variance was found to be important, particularly for tuber yield, in both methods with different material than that used in the Diallel design. From these analyses, it can be concluded that there is adequate additive genetic variance present in these particular families and perhaps in the AH population from which the sample was derived to allow for improvement of the population. The heritability values from both methods were comparable and were relatively high for a quantitative trait.

The next logical step to be examined would be the frequency of $2n$ gametes in the hybrid populations. This is a crucial step since the success of bilateral sexual tetraploidization depends on the presence of $2n$ gametes. Both $2n$ pollen and $2n$ eggs, in the hybrid populations were found to be present, making possible the use of the $2n$ gamete breeding method. As is demonstrated in Table 6 in the last section (Fertility and $2n$ gametes), several diplandrogyno-tetraploids can be generated from the present Group-hybrid populations or previously identified clones.

Up to this point, several important answers were obtained through this study: the crossability, and the male and female fertility of Gp. Andigena haploids were excellent; though heterosis was not expressed for tuber yield by AH hybrids, they did do so for dry vine and total dry matter weight; also TH hybrids demonstrated heterosis; considerable additive genetic variance was found to be present in the Gp. populations

as detected by the diallel design; and two other genetic designs, also revealed high additive genetic variances in a sample of Gp. Andigena haploid clones, and finally $2n$ gametes were found to be present in the hybrid populations.

In conclusion, the unique potato breeding scheme proposed by Mendiburu, Peloquin and Mok (1974), designed to capitalize on disomic inheritance, genetic diversity and bilateral sexual polyploidization, comes close to being achieved with the cultivated potato Groups. The determination of the breeding value of Gp. Andigena haploids, extensively studied in this research, would be of priceless value to the $2n$ gamete approach in potato improvement.

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APPENDIX

1. Code for the Diallel design analyses (Table 1)

L = Locations 1, 2
R = Replications 1, 2, 3
F = Females 1, 2, 3, 4
M = Males 1, 2, 3, 4

2. Code for the Design I analyses (Table 2)

L = Locations 1, 2
M = Males 1, 2, 3
F/M = Females within males

3. Code for the parental clones analyses (Table 3)

L = Locations 1, 2
F/M = Females within males

TABLE 1 YIELD TRIAL DATA IN LBS/HILL - DIALLEL DESIGN

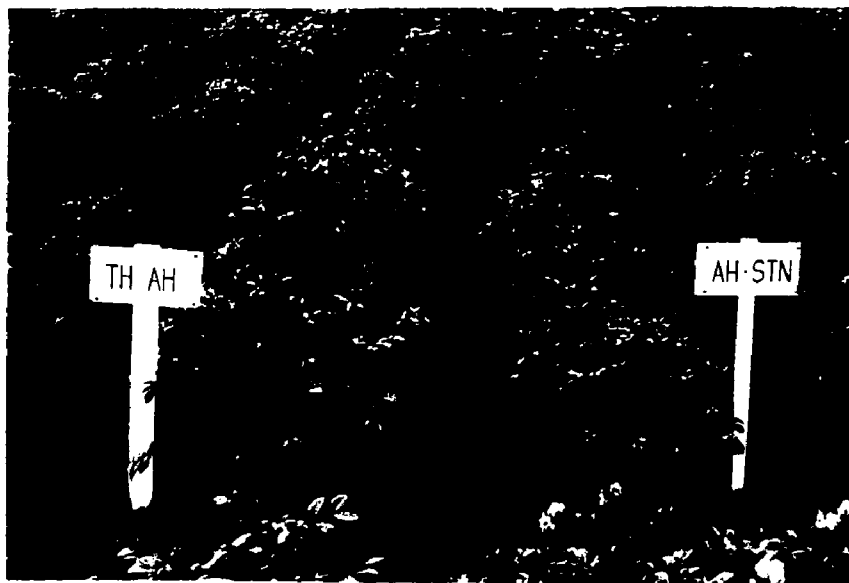
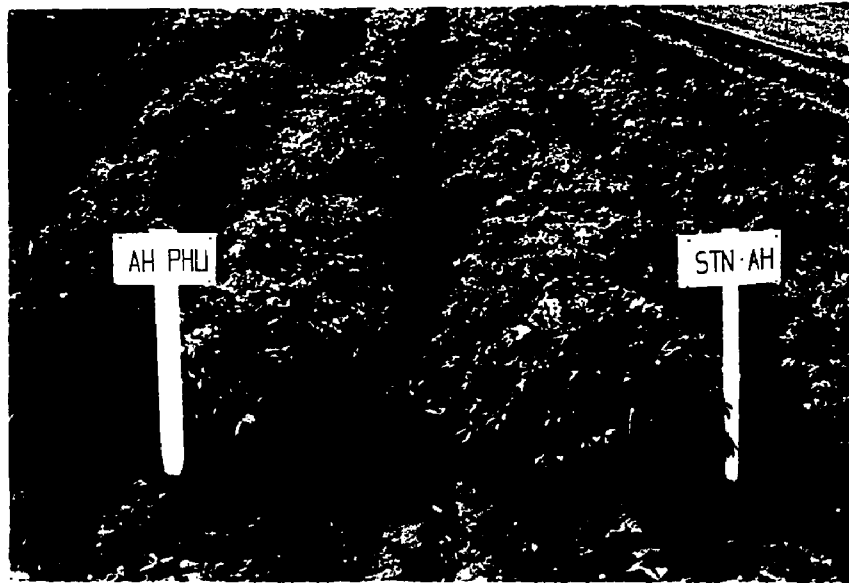
LRFH T, TUB VINE T+VN DRYV SPGR TSOL					LRFH T, TUB VINE T+VN DRYV SPGR TSOL						
1111	.34	3.67	4.01	.491.060	.54	2111	.39	1.74	2.14	.331.078	.40
1211	.21	3.99	4.20	.481.063	.51	2211	.92	1.48	2.40	.311.067	.47
1311	.23	5.27	5.50	.591.059	.62	2311	.37	1.70	2.06	.341.073	.41
1112	.71	3.07	3.78	.441.064	.56	2112	.68	.96	1.64	.211.079	.34
1212	.90	3.84	4.74	.561.068	.71	2212	.76	.93	1.69	.231.072	.37
1312	1.18	3.53	4.71	.431.067	.63	2312	.77	.93	1.70	.221.079	.37
1113	.61	3.11	3.92	.461.067	.59	2113	.58	1.32	1.90	.261.072	.37
1213	.76	4.44	5.22	.601.066	.78	2213	.53	1.52	2.05	.351.080	.40
1313	.78	3.72	4.50	.621.076	.77	2313	.46	1.68	2.14	.291.075	.40
1114	.59	4.22	4.82	.581.065	.68	2114	.44	1.32	1.76	.271.068	.35
1214	.39	5.22	5.60	.631.060	.69	2214	.38	1.26	1.65	.321.064	.43
1314	.53	4.02	4.56	.641.057	.72	2314	.41	1.58	1.99	.361.068	.44
1122	1.25	2.95	4.21	.441.065	.65	2122	1.14	.73	1.80	.161.075	.37
1222	1.14	3.01	4.15	.331.063	.51	2222	1.33	1.37	2.69	.371.073	.61
1123	2.01	2.76	4.78	.391.067	.73	2322	1.34	1.19	2.53	.261.081	.53
1223	1.66	3.44	5.10	.371.068	.65	2123	1.47	1.14	2.61	.231.078	.51
1323	1.69	4.33	6.02	.461.063	.74	2223	1.71	1.08	2.78	.241.080	.58
1124	1.19	3.68	4.87	.491.060	.67	2323	1.36	.99	2.35	.211.076	.47
1224	1.58	3.84	5.43	.461.064	.74	2124	1.06	.94	1.99	.201.074	.40
1324	1.55	3.54	5.09	.471.060	.71	2224	1.14	1.47	2.61	.291.071	.49
1133	1.07	3.53	4.60	.471.069	.66	2324	1.30	1.07	2.37	.271.074	.51
1233	.91	3.36	4.29	.461.067	.61	2133	.66	1.01	1.66	.221.066	.33
1144	.76	4.19	4.95	.511.056	.62	2233	.60	.92	1.53	.191.075	.30
1244	.86	4.30	5.16	.621.051	.74	2333	.64	1.07	1.72	.221.080	.35
1344	1.03	3.56	4.59	.541.053	.68	2144	.61	1.34	1.95	.271.052	.30
						2244	.68	1.17	1.85	.341.065	.45
						2344	.46	1.28	1.74	.291.063	.36

TABLE 2 YIELD TRIAL DATA IN LBS/MILL - DESIGN 1

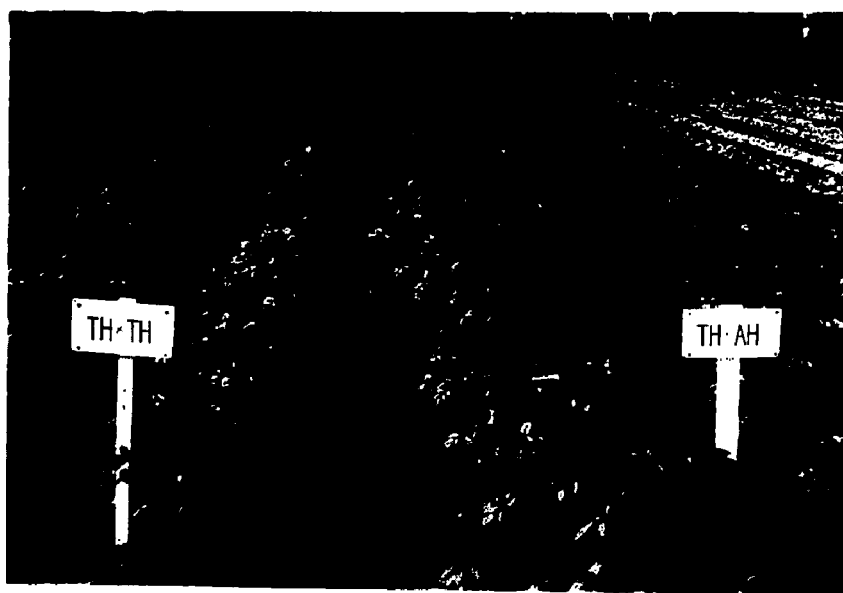
LMF/M	TURM MT.	VINE MT.	TURM+VINE MT.	DRY VINE MT.	SPEC. GRAV.	TOT. SUIND								
I	II	III	I	II	III	I	II	III						
11 2	10	05	34 3.10	3.67	4.10	3.29	3.72	4.48	41	49	561.0411.0691.066	43	50	62
11 4	40	12	20 3.26	4.15	2.18	3.66	4.27	2.36	44	53	311.0761.0651.065	52	55	34
11 5	11	16	09 5.27	4.49	4.93	5.36	5.04	5.02	65	73	641.0501.0141.060	67	73	65
11 6	11	20	10 2.97	2.69	3.00	3.08	3.09	3.10	42	43	401.0411.0341.060	44	45	42
12 1	37	43	66 4.02	4.68	3.97	4.38	5.11	4.63	58	72	641.0571.0541.056	63	78	74
12 2	12	16	14 3.21	3.75	3.30	3.33	3.32	3.43	50	57	491.0421.0511.056	52	59	51
12 3	44	42	20 3.67	3.94	2.99	4.11	4.37	3.14	54	56	421.0571.0591.058	61	62	45
12 4	17	32	26 5.21	5.25	3.64	5.38	5.57	3.90	60	81	361.0711.0601.068	63	86	40
12 5	41	20	26 3.87	4.90	4.39	4.28	5.10	4.65	56	74	671.0431.0541.060	63	77	78
12 6	10	37	31 5.84	4.81	4.86	5.98	5.17	5.16	79	83	661.0631.0411.062	81	89	71
12 7	74	29	43 3.65	4.00	4.92	4.39	4.29	5.34	57	50	661.0691.0641.063	70	55	73
12 8	45	24	28 3.90	4.53	4.26	4.35	4.74	4.54	52	57	541.0751.0441.072	60	61	61
12 9	23	30	26 5.17	5.72	4.81	5.40	6.01	5.09	79	83	691.0441.0401.064	83	88	73
12 10	30	22	22 3.46	4.71	4.63	3.75	4.93	4.64	53	66	661.0601.0541.055	54	69	69
13 1	40	55	43 3.39	3.44	3.81	4.40	3.99	4.24	58	51	541.0651.0891.065	61	63	61
13 2	40	43	72 4.25	4.65	3.52	4.65	5.04	4.23	66	72	551.0591.0421.069	72	79	67
13 3	56	44	37 2.60	2.73	2.38	3.16	3.57	2.75	41	44	351.0441.0691.070	51	59	41
13 4	55	34	49 2.93	4.78	3.61	3.48	5.12	4.10	37	74	481.0711.0441.066	47	80	56
13 5	64	19	3.19	2.61	3.08	3.20	3.20	3.67	46	43	1.0781.064	46	50	56
13 6	69	30	59 4.24	3.95	3.08	4.92	4.25	3.67	64	48	401.0721.0601.066	76	53	50
13 7	70	38	37 1.28	1.38	1.42	1.98	1.75	1.74	21	23	241.0831.0731.078	35	30	31
21 1	23	34	16	1.39	1.22	1.96	1.73	1.34	24	31	301.0441.0741.066	30	37	33
21 2	31	46	1.14	1.22	1.55	1.45	1.70	2.04	34	26	361.0731.0721.063	40	35	44
21 3	35	26	44 1.17	1.46	2.17	1.53	1.73	2.41	27	36	451.0751.0731.079	34	41	50
21 4	40	58	61 1.20	1.24	1.43	1.60	1.82	2.04	35	26	311.0741.0741.068	43	37	41
21 5	40	29	34 2.11	1.71	2.41	2.51	1.99	2.75	26	30	521.0501.0641.077	31	44	56
21 6	42	21	42 1.18	1.27	1.33	1.60	1.49	1.75	26	36	441.0421.0541.071	33	42	60
22 1	43	19	41 1.02	1.54	1.48	1.45	1.95	1.87	26	36	311.0411.0601.069	37	38	40
22 2	34	45	51 1.41	1.39	1.50	1.75	1.84	2.01	32	30	321.0461.0441.063	30	34	40
22 3	34	34	49 1.02	1.36	1.74	1.56	1.70	2.23	21	28	321.0461.0441.063	30	34	40
22 4	71	61	67 1.92	1.57	1.74	2.64	2.18	2.40	41	33	371.0401.0761.071	55	44	49
22 5	58	48	52 1.61	1.42	1.63	2.18	1.90	2.15	19	32	341.0401.0541.059	26	39	42
22 6	54	52	36 1.61	1.65	2.73	2.14	2.17	3.09	32	35	331.0561.0431.064	40	43	59
22 7	64	58	73 1.51	1.44	1.48	2.15	2.01	2.21	33	34	281.0711.0711.072	44	44	41
22 8	47	56	69 1.47	1.48	1.56	1.94	2.03	2.25	32	44	381.0401.0701.083	41	58	52
22 9	58	49	60 2.16	1.60	2.29	2.73	2.09	2.90	54	27	441.0411.0691.064	67	35	54
22 10	34	51	36 1.47	2.14	1.27	1.75	2.65	1.63	27	37	231.0641.0631.064	33	45	29
22 11	47	39	1.97	1.41	1.44	1.19	1.19	1.19	18	18	1.0671.073	26	25	29
23 1	59	48	57 1.18	1.34	1.26	1.77	1.62	1.63	26	32	221.0731.0711.070	37	40	32
23 2	53	57	49 1.29	1.46	1.92	1.62	2.02	2.40	31	30	471.0761.0701.070	41	40	56
23 3	59	63	64 1.06	1.04	1.14	1.65	1.87	2.40	24	25	241.0741.0621.054	35	42	36
23 4	54	59	98 1.62	1.46	1.51	2.17	2.04	2.49	32	31	341.0571.0671.071	40	41	51
23 5	50	62	51 1.33	1.37	1.16	1.43	1.99	1.67	33	26	241.0441.0741.076	41	39	34
23 6	63	76	55 1.26	1.44	1.41	1.89	2.20	1.96	25	27	251.0711.0701.076	36	40	34
23 7	51	42	46	1.56	1.10	1.07	1.96	1.56	13	16	301.0721.0741.076	22	24	39

TABLE 3 YIELD TRIAL DATA IN LBS/HILL - PARENTAL CLONES

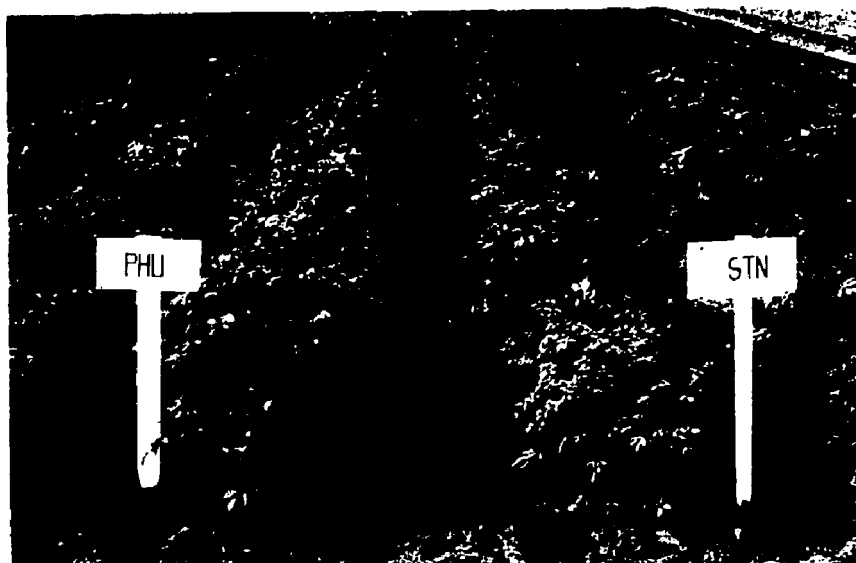
L F/M	TUBER WT.	VINE WT.	TUBER+VINE WT.	DRY VINE WT.	SPEC. GRAY.										
I	II	III	I	II	III										
11 3	.22	.22	.32	.12	.10	.30	.34	.53	.62	.04	.04	.061	.0621	.0641	.068
12 4	.08	.20	.38	3.64	4.12	3.98	3.72	4.32	4.36	.60	.64	.801	.0721	.0761	.081
1 5	.34	.03	.10	.48	.60	.63	.70	.70	.70	.13	.13	.201	.0681	.086	.1069
11 6	.04	.10	.06	5.74	7.04	7.42	5.80	7.14	7.48	1.00	1.06	1.121	.036	1.069	
11 7	.78	1.12	.66	2.21	2.96	2.40	3.88	4.08	3.06	.54	.40	.381	.0701	.0761	.067
1 8	.07	.15	.27	2.27	.53	.97	2.33	.68	1.23	.47	.10	.171	.0451	.0921	.100
12 9	.04	.52	2.02	2.26	1.28	2.00	2.78	1.80	.34	.38	.38	.241	.0881	.0871	.086
11 10	.52	.42	2.66	.14	1.58	3.18	.56	2.00	.52	.04	.04	.321	.0681	.0641	.068
13 11	.78	.72	.43	1.48	1.34	1.53	2.26	1.10	1.95	.28	.10	.281	.0741	.0651	.072
12 12	1.02	.36	.74	3.32	1.34	2.44	4.34	1.70	3.26	.72	.26	.401	.0721	.0671	.073
12 13	.08	.36	.15	.60	1.00	.65	.68	1.36	.80	.14	.20	.151	.0691	.0841	.053
21 1	.08	.14	.06	1.36	1.36	1.26	1.46	1.50	1.32	.34	.38	.361	.0601	.054	.061
21 3	.56	.48	.86	.44	.48	.42	1.00	.96	1.28	.10	.12	.171	.0671	.0681	.061
22 4	.52	.28	.33	1.86	1.14	1.40	2.34	1.42	1.73	.44	.30	.601	.0901	.0881	.076
2 5	.01	.03	.02	.33	.10	.10	.35	.13	.12	.08	.05	.041	.081	.0551	.061
21 6	.52	.48	.42	3.16	2.16	2.66	3.68	2.64	3.08	.80	.86	.801	.0561	.0551	.061
21 7	.68	.82	.70	2.20	1.28	1.96	2.88	2.10	2.72	.54	.32	.501	.0661	.0841	.079
21 8	.23	.63	.36	.15	.22	.38	.38	.90	.74	.05	.10	.101	.0761	.0831	.080
22 9	.28	.44	.42	.14	.14	.14	.42	.58	.56	.06	.06	.061	.0391	.0741	.072
21 10	.66	.76	1.20	2.06	.22	.98	2.72	.98	2.18	.58	.10	.341	.0501	.0501	.052
23 11	.64	1.08	.56	.78	.74	.26	1.46	1.82	.82	.16	.36	.101	.0521	.0501	.056
22 12	.76	.94	.98	3.36	2.74	2.40	4.12	3.68	3.30	.64	.62	.581	.0581	.0631	.059
22 13	.32	.22	.13	.90	.26	.67	1.22	.48	.80	.28	.08	.271	.0631	.0641	.080



Figures 1, 2. Hybrid families in plots at Sturgeon Bay (two rows per family).



Figures 3, 4. Hybrid families in plots at Sturgeon Bay.



Figures 5, 6. Hybrid families and, PHU and STN Group families in plots at Sturgeon Bay.

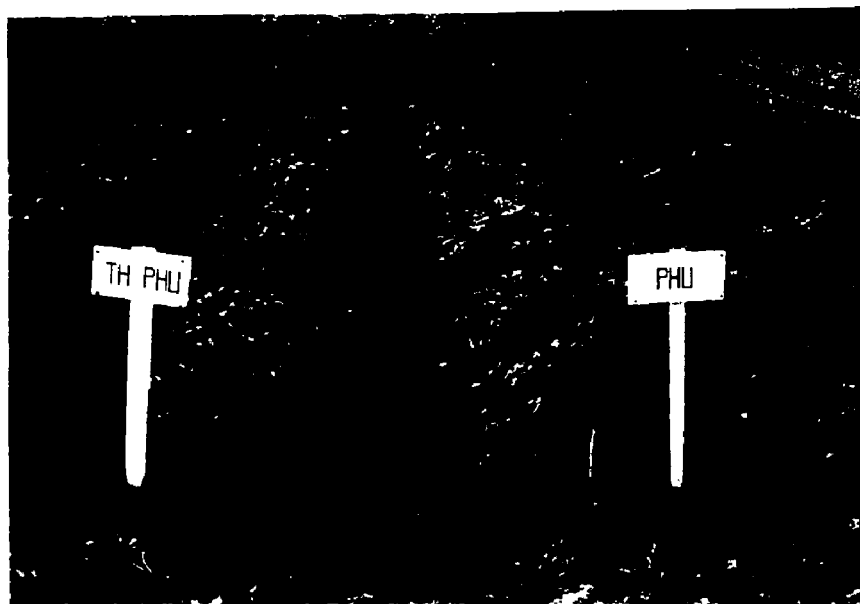


Figure 7. Hybrid family and PHU Group family in plots at Sturgeon Bay.

TITLE OF THESIS BREEDING POTENTIAL OF GROUP ANDIGENA HAPLOID POTATOES

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Major Department PLANT BREEDING & PLANT GENETICS

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SIGMA XI

CCLEGIO DE INGENIEROS DEL PERU

Publications _____

Three abstracts in American Potato Journal 1976, 78, 79.

One paper : Crossability of Gp. Andigena haploid potatoes in

American Potato Journal (recently accepted) 1979.

Date Junio 15, 1979.